Cooperative Sentinel Behaviour and its Vocal Coordination in Meerkats

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SUMMARY

A benefit of living in groups is the potential to evolve coordinated antipredator strategies. Sentinel behaviour is a form of coordinated vigilance behaviour, where usually one individual adopts a raised position and scans the environment for the presence of predators, while the rest of the group is foraging. All adult group members contribute to sentinel behaviour, however, the extent to which each individual acts as sentinel varies greatly. Understanding the specific underlying costs and benefits of cooperative behaviours to explain this variation among individuals, groups and populations has remained one of the major questions in the field of behavioural ecology. Another important aspect of cooperative behaviours is their coordination. Many animals evolved specific vocal signals to coordinate cooperative behaviours among group members. To fully understand the mechanism underlying the interaction between the producer of the signal and the receiver(s), it is fundamental to recognize the specific vocalisations involved, understand their function and information content as well as how this information is subsequently used by other group members to adjust their own behaviour accordingly.

In my thesis, I focused on cooperative sentinel behaviour in meerkats (*Suricata suricatta*). Sentinel behaviour is well suited to investigate the underlying costs and benefits of cooperation because it represents a combination of costly aspects, i.e. foregoing foraging, as well as beneficial aspects such as adopting a safe position, or potential information gathering or reputational aspects, which are not yet clear in meerkats. Moreover, meerkat sentinels produce six distinct sentinel call types, but little is known about the underlying reasons for this comparatively large sentinel call repertoire, the information that can be encoded therein and the use of this information by group members. Combining both aspects together, individual variation in cooperative behaviour as well as its vocal coordination, I aimed to improve our understanding of how social and environmental factors promote or constrain this cooperative behaviour and how they affect the extent and mechanisms underlying its vocal coordination.

The results suggest that the amount of sentinel behaviour an individual displayed was highly dependent on condition and predation risk. I found that during a drought - an extreme environmental condition with very low food availability - the extent of sentinel behaviour decreased significantly, especially in young individuals, small groups and groups with dependent young. The vocal coordination between sentinels and the rest of the group including the production of all six types of sentinel calls was already done by young meerkats when they first started to act as sentinels. Moreover, call rates and acoustic parameters showed little change with increasing age and experience. Quantifying whole sequences of sentinel calls produced during a sentinel bout revealed that the order of the call types was produced in a graded way and contained information about the identity of the caller. Testing whether the conveyed information about sentinel identity in calming sentinel calls was meaningful for the receivers resulted in clear

discrimination among signallers, whereby receivers relied most on calming calls produced by the most experienced sentinels and littermates. Ecological conditions, too, specifically drought condition, resulted in a flexible adjustment of the behavioural response of foraging group members when hearing sentinel calls.

The research presented in this thesis provides strong evidence that sentinel behaviour as well as its vocal coordination are driven by a strong trade-off between the costs of foregoing foraging and the risk of being predated. Comparison with other cooperative breeders inhabiting less-constraining environments will provide valuable insight into variation in cooperative tasks among individuals, as well as the influence of social and environmental variables on vocal complexity.

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General Introduction

Living in Groups

Many animals live in stable social groups ranging from small family units including a breeding pair and their offspring – a system seen in many bird species but also some mammals - up to large groups of animals such as fish schools or bird flocks. Regardless of the vast differences in group size and kinship structures, social groups can be generally defined as a group of conspecifics, which co-occur spatially and temporally as a result of mutual attraction to each other rather than the attraction to the same resource or physical condition (Parrish and Hamner, 1997; Pitcher and Parrish, 1992; Wilson, 1975). The high abundance of group-living across taxa indicates that the net benefits of close association with conspecifics exceed the potential costs, which include increased disease transmission (Hoogland, 1979; Hoogland and Sherman, 1976), increased competition for resources and reproduction (Hoogland, 1979), or increased risk of infanticide (Hoogland, 1985). In contrast, there are two main factors, which are thought to be crucial drivers for grouping: enhanced access to resources and decreased predation risk (Davies et al., 2012; Hamilton, 1971; Kenward, 1978; Krause and Ruxton, 2002; Macdonald, 1983; Zoratto et al., 2009). The decrease in predation risk is based on several, non-mutually exclusive mechanisms including increased predator detection (Kenward, 1978; Pulliam, 1973), dilution of individual predation risk as a proportion of group size (Hamilton, 1971; Pitcher and Parrish, 1992), the difficulty to single out and attack an individual (Neill and Cullen, 1974) and the potential to evolve coordinated group defence strategies (Birkhead, 1977; Kruuk, 1964).

Evolution of Cooperation

As a consequence of group-living, some species have evolved cooperation among group members in order to coordinate certain behaviours, such as predator avoidance behaviours, offspring care or food acquisition (Clutton-Brock, 2016; Silk, 2007). Cooperative behaviours can be divided into two categories: mutualistic behaviours which generate direct fitness benefits to cooperators through its benefit to others (West et al., 2007) and altruistic behaviours, during which a cooperator pays a cost for another individual to receive a benefit (Hamilton, 1964; Nowak, 2006; West et al., 2007). Since selection is based on competition between individuals – whereby the fittest individuals display the highest survival and contribute most to future generations – explaining the evolution of costly forms of cooperative behaviours presented a major challenge in behavioural ecology since the days of Darwin (Darwin, 1859). Several mechanisms have since been proposed that show how natural selection can lead to the evolution of cooperation while

maintaining the underlying competitive character. Hamilton's rule states that selection can favour cooperation if the cooperator and the receiver are genetic relatives, thus providing indirect genetic benefits for the cooperator (Hamilton, 1964). However, cooperation is not only limited to relatives, but also occurs between unrelated individuals within and between groups (Dugatkin, 1997), or even between individuals of different species (Trivers, 1971; Trivers, 2006). When cooperator and receiver repeatedly interact with each other, direct reciprocity including tit-for-tat (Axelrod, 1984; Axelrod and Hamilton, 1981), generous tit-for-tat (Nowak and Sigmund, 1992) and win-stay-lose-shift theories (Nowak and Sigmund, 1993), have been developed to explain the evolution of cooperation among unrelated individuals (Nowak, 2006). Here, an individual's decisions whether to cooperate or not is based on the previous interactions with the receiver (Trivers, 1971; Trivers, 2006; Wilkinson, 1988). Furthermore, indirect reciprocity, characterised by an individual A helping B while C is watching and resulting in increased chances of C helping individual A at a later stage, thus representing reputational aspects, successfully explains cooperation where pairs only meet randomly (Nowak, 2006; Nowak and Sigmund, 1998).

In addition to the underlying mechanism of cooperation, environmental circumstances highly affect the evolution and extent of cooperation. Territory quality, access to breeding opportunities and resource availability are important factors influencing individuals' decisions to invest more into cooperative behaviours or alternatively into their own survival and reproduction (Komdeur, 1992). In particular cooperative breeding – a social system where only the dominant pair reproduces, and other group members forego reproduction and help raise the dominant pair's offspring (Gaston, 1978; Solomon and French, 1997; Stacey and Koenig, 1990) – has been demonstrated to be closely linked to environmental conditions (Arnold and Owens, 1999; Komdeur, 1992; Rubenstein, 2011; Stacey and Koenig, 1990). Recent work on the global occurrence of cooperative breeding in birds and mammals demonstrated that cooperative breeding is closely linked to arid habitats with high variation in rainfall and temperatures across years (Jetz and Rubenstein, 2011; Lukas and Clutton-Brock, 2017). The resulting unpredictability in resource availability has likely affected the costs and success rates of dispersal (Komdeur, 1992) and independent reproduction (Rubenstein, 2011). In contrast, the benefits of staying with the natal group and engaging in territory defence (Gaston, 1978; Shen et al., 2017) as well as gaining mutualistic and indirect genetic benefits by contributing to alloparental care (Clutton-Brock, 2002), are likely to be increased under harsh conditions, facilitating the emergence of cooperative breeding.

Variation in contribution to cooperative activities varies substantially between species, populations within species, groups as well as between members of the same group (Bergmüller et al., 2010; Clutton-Brock, 2016). Most animal groups are not composed of uniform individuals, but instead contain individuals of different age, sex and dominance categories. These differences between group members result in specific cost-benefit ratios for each category, which often

underly individual differences in the amount of contribution to cooperative behaviours (Barclay and Reeve, 2012; Clutton-Brock et al., 2000; Clutton-Brock et al., 2002; Kern and Radford, 2013; Russell, 2004). Understanding the specific underlying trade-offs each group member faces is necessary to explain variation in cooperation within and between groups and populations and, ultimately, advances our understanding of the selective conditions under which cooperation evolved and how it is maintained.

Vocal Coordination of Group Living and Cooperative Behaviours

Living in groups requires individuals to coordinate their daily activities across different contexts including coordination of different individuals' foraging needs and preferences while maintaining group cohesion, coordination of cooperative behaviours, or warning group members of predators in order to initiate individual flight responses or a coordinated group defence. Besides olfactory, visual or electric communication, one of the most common coordination mechanisms in animals is vocal communication. Here, a signaller produces an acoustic signal, which is perceived by the receiver and leads to a change of the receiver's behaviour, resulting in a net benefit for both parties (Bradbury and Vehrencamp, 1998). Acoustic signals vary substantially in their structure, function as well as information content depending on the context in which they are produced. Short distance contact calls, for example, are soft vocalisations between members of a group, or between mothers and their offspring, which facilitate spatial coordination between the caller and the receivers over short distances (Fischer et al., 2001; Gall and Manser, 2017; Kondo and Watanabe, 2009). In contrast, some calls related to male quality or territorial ownership such as a roaring of lions or red deer stags can be very harsh in their structure and heard over long distances (Clutton-Brock and Albon, 1979; Pfefferle et al., 2007; Reby and McComb, 2003).

To understand the information encoded in acoustic signals – and therefore their function and evolutionary background – it is essential to investigate both the contexts resulting in the production of the signal as well as the response of the receivers when exposed to the signal (Macedonia and Evans, 1993; Marler et al., 1992). For example, alarm calling behaviour where prey animals across many taxa produce warning or alarm signals when they spot a predator, which lead to appropriate flight responses or coordinated defence strategies of group members (Caro, 2005; Sherman, 1977). Although elicited in the same context, the information encoded in alarm calls and the according responses expressed by the receivers can be grouped into two distinct categories. Some alarm calls reflect the emotional or internal state of the calling individual (Gill and Bierema, 2013; Marler et al., 1992). In marmots, for example, alarm calls are closely associated with the caller's perceived risk, which varies with the urgency of the situation, and receivers respond with a general flight response, independent of alarm call type (Blumstein, 1999; Blumstein and Armitage, 1997). In contrast, functionally referential alarm calls refer to specific

external objects or events in the environment of the caller (Gill and Bierema, 2013; Marler et al., 1992). Vervet monkeys (*Chlorocebus pygerythrus*) produce different types of alarm calls for leopards and for eagles and moreover, in the absence of a predator, hearing a leopard alarm call results in Vervet monkeys moving into trees, while playbacks of eagle alarm calls made them look up and run to shelter into bushes (Seyfarth et al., 1980). Thus, even in the absence of a predator, these calls contain indexical information about the type of predator and elicit distinct behavioural responses (Seyfarth et al., 1980).

Besides information about the internal state of the caller and indexical information about external objects or events in the animals' environment, some calls contain (additional) information such as caller identity (Robisson et al., 1993), group identity (Boughman, 1997), or caller characteristics including age, sex or dominance status (Bouchet et al., 2010; Briefer and McElligott, 2011a; Vannoni and McElligott, 2007). Information about caller characteristics allow receivers of the signal to adjust their behavioural response accordingly. For example, individual specific contact calls facilitate parent offspring recognition in colonial or group-living species, resulting in reduced likelihood of misdirected parental care as well as increased offspring survival (Balcombe, 1990; Balcombe and McCracken, 1992; Sayigh et al., 1990). Calls containing information about body size, such as the roaring of red deer stags (*Cervus elaphus*) can be used by competitors to assess the competitive ability of the caller, as well as by potential mates during mate choice (Charlton et al., 2007; Clutton-Brock and Albon, 1979; Reby et al., 2005).

Vocal signals represent an important source of social information, which can be used by other group members in order to acquire information about their environment. Using social information by monitoring other group members behaviour or calls – in contrast to acquiring personal information about foraging opportunities, mate quality or predation risk – has several benefits including faster transfer of information, enhanced skill learning and lower costs of information acquisition (Danchin et al., 2004; Galef and Giraldeau, 2001; Giraldeau, 1997; Valone, 2007; Valone and Templeton, 2002). On the other hand, social information can also be costly as it holds the risk to be inaccurate, irrelevant or deceptive (Beauchamp and Ruxton, 2007; Giraldeau et al., 2002). To minimize the potential costs of social information, some animals assess the quality and relevance of the provided information by relating information about the calling individual to past performances of that individual, usually referred to as reliability assessment (Blumstein et al., 2004; Cheney and Seyfarth, 1988; Hare and Atkins, 2001). For example, after hearing alarm calls from unreliable individuals, yellow-bellied marmots (*Marmota flaviventer*) spend less time foraging and more time assessing the relative risk compared to when they hear alarm calls from reliable callers, which have produced more reliable signals in past predator encounters (Blumstein et al., 2004).

Sentinel Behaviour and Calls

Sentinel behaviour is a form of coordinated vigilance behaviour, where usually one individual adopts a raised position and scans the environment for the presence of predators, while the rest of the group is mostly foraging (reviewed in Bednekoff, 2015). Sentinels occur mainly in cooperative breeding species, including social mongooses (Clutton-Brock et al., 1999b; Rasa, 1986), babblers (Ridley and Raihani, 2006; Wickler, 1985; Zahavi, 1990) and primates (Hall, 1960; Horrocks and Hunte, 1986). Sentinels have been demonstrated to detect predators more frequently and from greater distances than foraging group members (Manser, 1999; Wright et al., 2001b) and foraging group members show a higher foraging efficiency when a sentinel is on guard (Hollen et al., 2008a; Manser, 1999). Therefore, sentinel behaviour minimizes the trade-off between vigilance and foraging behaviour for the other group members. Although most adults of a group contribute to sentinel behaviour, there is substantial variation in the amount of sentinel behaviour among members of the same group as well as between groups and populations. The underlying reasons for the large observed variation in cooperative sentinel behaviour remain unclear.

In most species known to have a sentinel system, sentinels produce specific calls informing the rest of the group about the presence of a guard, as well as in some cases information about the perceived risk (Hollen et al., 2008a; Kern and Radford, 2013; Rasa, 1986). In dwarf mongoose (*Helogale parvula*), the so called "Watchman's song" describes the continuous production of a single sentinel call type, whereby the call rate varies with perceived risk (Kern and Radford, 2013; Rasa, 1986). In contrast, meerkat sentinels continuously produce multiple different sentinel call types (Manser, 1999), and in case of a detected predator, they emit functionally referential alarm calls including information about the type of predator as well as the urgency of a response (Manser, 2001; Manser et al., 2001; Manser et al., 2002). Previous work on meerkat sentinel calls has identified six different call types (Manser, 1999). The sentinel calming calls are produced when no predator is in sight and function as an 'all-clear' call, leading to an increase in foraging behaviour and a decrease in vigilance behaviour by the rest of the group (Rauber and Manser, 2017). Sentinel warning calls, on the other hand, are emitted when the sentinel individual experiences an increase in perceived risk and function as a pre-stage of alarm calls, leading to an increase in vigilance behaviour and a decrease in foraging by receivers (Rauber and Manser, 2017). Therefore, meerkat sentinels inform the other group members constantly about subtle changes in the perceived predation risk, which then leads to behavioural adjustments by foraging group members.

Research Aim

The general objective of this dissertation is to improve our understanding of how social and environmental factors influence both the contribution to cooperative sentinel behaviour and the acoustic coordination between the sentinel and the rest of the group. Despite the increasing amount of data on sentinel behaviour across taxa, we still do not understand the underlying costs and benefits for the individual acting as sentinel guard. Investigating the extent and variation with which individuals within and between groups and populations contribute to sentinel behaviour is a key step in understanding the potentially individual specific costs and benefits involved. I investigate this by using long-term observational data collected over 20 years, allowing me to address the large variation in individual contribution to sentinel behaviour of hundreds of individuals across years and ultimately across individuals' lifespans.

Using acoustic recordings and playback experiments I aim to enhance our understanding of the proximate mechanisms used by the sentinel to provide information about the current perceived risk as well as the use of this information by foraging group members. Having six distinct sentinel call types, meerkat sentinels seem to possess a more complex acoustic system to coordinate sentinel behaviour compared to other species' sentinel systems. Understanding the underlying causes and consequences of having such a complex vocal coordination of sentinel behaviour in meerkats allows us to further advance our understanding of the function and mechanisms of complex acoustic signals in animal communication systems, as well as under which selective conditions they can evolve. In particular, I am focusing on call type use and the extent of individual distinctiveness throughout the ontogenetic development of sentinel calling in young individuals, the structure and information content of complete sentinel sequences across all age classes and lastly how receivers adjust their behavioural response to sentinel calls dependent on the identity of the caller as well as the current environmental conditions.

By applying this complementary approach, we will have a clearer understanding of how the biotic and abiotic environment constraints or promotes this cooperative behaviour. Moreover, advancing our knowledge about the function of sentinel calls, the complexity of call sequences, ontogenetic development and response to calls by conspecifics allows us detailed insight into the proximate mechanism of the coordination of sentinel behaviour. All chapters together improve our understanding of how cooperative sentinel behaviour evolved, is maintained and coordinated among group members.

Study Species and Site

Meerkats

Meerkats are small (adults are about 800g), highly sociable mongoose (*Herpestidae* family), occurring in arid, semi-desert areas of the Kalahari Desert in southern Africa (Doolan and Macdonald, 1996). They live in groups ranging from 3 up to 50 individuals composed of different age classes (pups ≤ 3 months, juveniles >3–6 months, subadults >6–12 months, yearlings >12–24 months, and adults > 24 months; Clutton-Brock et al., 1999a). Meerkats are cooperative breeders resulting in stable groups consisting of a dominant, reproductive pair and several subordinates, which help to rear the dominant pair`s offspring by providing them with food and protection (Clutton-Brock et al., 2001b; Clutton-Brock and Manser, 2016; Clutton-Brock et al., 1999). Meerkats are diurnal and spend the majority of the day foraging as a cohesive unit - often moving within a distance of 20–50 meters from the closest shelter (Manser and Bell, 2004) - in search for invertebrates such as millipedes, larvae or scorpions as well as more rarely small vertebrates including geckos, lizards, small snakes, or rodents (Doolan and Macdonald, 1996). Active foraging often involves digging in the soil for prey, which prevents them from visually scanning their surroundings for the presence of aerial predators, such as martial eagles (*Polemaetus bellicosus*), and terrestrial predators, such as jackals (*Canis mesomelas*) (Clutton-Brock et al., 1999a). The combination of the open environment, the inability to scan it during foraging and the variety of predators led to the evolution of an elaborate sentinel system (Clutton-Brock et al., 1999b). Meerkat sentinels continuously produce six types of sentinel calls, informing other group members about the current perceived predation risk, as well as functionally referential alarm calls when a predator is spotted (Manser, 1999, 2001; Manser et al., 2001; Manser et al., 2002; Rauber and Manser, 2017).

Kalahari Meerkat Project

The data for this thesis has been collected at the Kalahari Meerkat Project (KMP), located at the Kgalagadi Transfrontier Park (KTP; 1993-1996) and the Kuruman River Reserve (KRR; since 1996) in the southern Kalahari Desert, Northern Cape, South Africa (for more information about habitat at the study site, see Clutton-Brock et al., 1999a; Russell et al., 2002). I used long term data from both study populations as well as recordings and playback experiments conducted between 2014 and 2017 at the KRR. Both study sites consisted of the same semi-arid habitats (Clutton-Brock et al., 1999; Doolan and Macdonald, 1996). However, predation risk at the KTP was much higher compared to the KRR (total number of predators per 100 hours of observations was 20.29±11.24 in the KTP and 4.49±6.38 at the KRR), resulting in significantly different mortality rates (Clutton-Brock et al., 1999a). As part of the KMP's long-term data collection, all group

members were uniquely dye marked to allow individual recognition, and one or two individuals of each group were fitted with radio-collars to facilitate localization of the group (Jordan et al., 2007). All groups were habituated to close human observations and to the microphone and playback equipment, allowing us to perform recordings and playbacks within a distance of 0.5 m and 1-2m, respectively, to the test subjects.

Thesis Outline

The aim of this dissertation is to investigate how social and environmental factors influence different aspects of cooperative sentinel behaviour and its vocal coordination. By focusing on ultimate and proximate aspects of this cooperative behaviour I aim to improve our understanding of the large variation in contribution to sentinel behaviour among individuals, groups and populations, and how group members use vocal signals with multiple levels of information content and complexity to coordinate it.

Chapter 1 explores the large individual variation in contribution to cooperative sentinel behaviour within and between groups. Addressing differences across individuals in the amount of cooperative behaviour they show is crucial to understand the underlying costs and benefits involved and ultimately the evolution and maintenance of cooperation. This chapter addresses how social factors including age, sex, dominance status, group size and the presence of littermates, as well as environmental factors, in particular, predation risk, influence contribution to sentinel behaviour across individuals, different groups and two different populations. I present the three current hypotheses about the evolution of sentinel behaviour and evaluate them using a large dataset of over 20 years, which allows me to examine how much time individuals invest into sentinel behaviour across years and ultimately across individuals' lifespans.

Chapter 2 addresses the importance of environmental factors, specifically rainfall, on contribution to sentinel behaviour and the responsiveness of foraging group members to sentinel calls. As cooperative breeders, meerkats have evolved under harsh conditions with high variation in rainfall and temperatures. Under normal conditions costly cooperative behaviours are conditional on an individual's food intake. However, the effect of naturally occurring extreme environmental conditions on the persistence of costly forms of cooperative behaviours and their vocal coordination remain unknown. In this study, I compare individual contributions to sentinel behaviour across three different environmental conditions: wet, dry and drought. Besides potential change in investment to cooperative behaviours as a result of drought, we compared responsiveness to sentinel calls during a wet condition and a drought condition, investigating the consequences of the environment on the responsiveness to certain types of sentinel calls.

Focusing specifically on the vocal coordination of sentinel behaviour, in **Chapter 3**, I explore the ontogenetic development of sentinel calling behaviour in young meerkats. Knowing the different functions of the sentinel calming calls and sentinel warning calls allow me to address questions about when and how young meerkats start producing the different types of sentinel calls and whether they undergo acoustic development. While sentinel calming calls refer to the absence of a predator, sentinel warning calls act as general pre-stages of alarm calls, thus potentially resulting in differences across ontogenetic development. I test when young animals begin to go on guard, when the different types of sentinel calls can be found in the vocal repertoire and finally I measure a set of acoustic parameters quantifying the amount of individuality from when they first started to go on guard until reaching adulthood.

Chapter 4 moves from the production of single sentinel call types to investigating complete sentinel sequences produced during a sentinel bout. Animal vocal sequences are used in many different contexts and thus take on many different functions. Meerkat sentinels continuously produce long sequences composed of the six described sentinel calls, but despite knowing the functions of some of the sentinel call types, nothing is known about the ordering of the sentinel call types and its potential information content. This study tests if the order of the different sentinel call types and alarm calls is produced in a graded way within longer call sequences and whether sentinel sequences contain additional information about group and/or caller identity, rank, sex or age.

Chapter 5 investigates how social factors, such as age, dominance and experience influence other group members' responsiveness to sentinel calls. Sentinel calls represent an important source of social information for other group members that provides information about the temporary perceived predations risk experienced by the sentinel individual. However, social information can be costly when the provided information is inaccurate or irrelevant for receivers. Using playback experiments coupled with focal observations of the receivers of the signal, this study examines how social factors influence other group members decisions to rely on the provided information or when it is safer to switch to personal information.

CHAPTER 1

1. ECOLOGICAL AND SOCIAL EFFECTS ON INDIVIDUAL VARIATION IN SENTINEL BEHAVIOUR IN MEERKATS

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ABSTRACT

Individual differences in the contribution to cooperative behaviours are common in many social mammals and birds, yet the reasons for this variation are not fully clear. In this study we analysed the large variation found in acting as a sentinel – a coordinated vigilance behaviour – between individuals and groups of two populations of meerkats (*Suricata suricatta*). We determined the role of social and ecological factors in explaining this variation and assessed the evidence for the three most recently discussed theories on the evolution of sentinel behaviour: the 'state dependency hypothesis' suggesting that sentinel behaviour is highly condition dependent; the 'social display hypothesis' stating that acting as a sentinel is a sign of high quality and leads to social or sexually selected direct benefits; and the 'information acquisition hypothesis' implying for males to gain information on extra-group mating opportunities. Our results support findings

across species that variation in sentinel behaviour is mainly condition and risk dependent. However, we found some indication that competition among same-sexed, same-aged females led to an increase in sentinel behaviour, potentially representing a social display of good condition or competitive abilities. In males, we demonstrate that temporary prospecting behaviour and inter-group encounters led to a decrease in contribution to sentinel behaviour, contradicting the 'information acquisition hypothesis', but further supporting the 'state dependent hypothesis'. We conclude that sentinel behaviour is the result of a finely balanced trade-off between the benefits of maximizing foraging time for the sentinel as well as the group and the costs of being exposed to predators. Social aspects seem to play a secondary role and come into play only when conditions allow them to do so. Quantifying individual contribution in cooperative behaviours across life-history stages, within and between groups and populations, is crucial to identify the causal and functional mechanisms controlling cooperation in social mammals.

Key words: cooperation, cooperative breeders, individual variation, sentinel behaviour

INTRODUCTION

Individual differences in the contribution to cooperative behaviours are highly pronounced in many social mammals and birds, yet the reasons for this variation are not fully clear. The extent to which different individuals within and between groups and populations of a species contribute to cooperation depends on the specific cost-benefit balance experienced while performing a specific type of cooperation. Consequently, variation in cooperative behaviour has been reported to be related to demographic factors, including group size and composition (Clutton-Brock et al., 1999b; Ridley and Raihani, 2007), as well as individual characteristics including age and sex (Clutton-Brock et al., 2002). Besides these social factors, variation in cooperative behaviour can be associated with differences in environmental factors including predation risk (Clutton-Brock et al., 1999b; Ridley et al., 2010), habitat (Hollen et al., 2011b) and climatic conditions (Rauber et al., 2019b; Wiley and Ridley, 2016).

Differences in individual contribution to specific cooperative behaviours in response to social and ecological influences provide valuable insights into the underlying evolutionary mechanisms that have been suggested to explain the evolution of costly forms of cooperative behaviours. Altruistic behaviour in animals is typically explained by indirect fitness benefits gained from cooperating with relatives (Clarke, 1984; Hamilton, 1964; Komdeur, 1994; Owens and Owens, 1984). Alternatively, individuals may gain direct benefits via group augmentation,

where individuals benefit from living in larger groups and thus everybody contributes as much as possible (Kingma et al., 2014; Kokko et al., 2001). Moreover, under social and sexual selection some individuals' contribution to cooperative behaviours increases their chances of receiving help (Kern and Radford, 2018; Schweinfurth and Taborsky, 2018) or being chosen as a mate (Zahavi, 1990; Zahavi and Zahavi, 1999; reviewed in Covas and Doutrelant, 2018).

Sentinel behaviour is a coordinated vigilance behaviour mostly known in cooperatively breeding species (Bednekoff, 2015), including birds (babblers: Bell et al., 2010; Wickler, 1985; Wright et al., 2001a, scrub jays: McGowan and Woolfenden, 1989) and mongooses (meerkats: Clutton-Brock et al., 1999b; Rasa, 1986). The sentinel individual ceases foraging and moves to an elevated position, scanning their surroundings for predators while the rest of the group continuous to forage (Bednekoff, 2015; Horrocks and Hunte, 1986; McGowan and Woolfenden, 1989). Acting as a sentinel has costs, as it is incompatible with foraging, though these energetic costs may not be large, since satiated individuals commonly contribute disproportionately (Bednekoff, 1997, 2001; Wright et al., 2001c). Moreover, for some species, an increased risk of predation while on sentinel guard has been documented (Rasa, 1987b; Ridley et al., 2013). In contrast, in other species it has been suggested that the sentinel takes on the safest location there is when not foraging (Bednekoff, 1997; Clutton-Brock et al., 1999b), and the presence of a sentinel increases the probability that predators will be detected (McGowan and Woolfenden, 1989; Ridley et al., 2010). Furthermore, sentinels emit a variety of different call types that convey information about their presence as guard (Hollen et al., 2011a; Manser, 1999; Rasa, 1986; Rauber and Manser, 2017), and they alert the group to approaching predators, enabling the rest of the group to reduce their level of vigilance and to forage more effectively (Hollen et al., 2008a; Manser, 1999; McGowan and Woolfenden, 1989; Rasa, 1989; Ridley et al., 2010).

As sentinel behaviour is mostly shown by cooperative breeders, where kinship between group members is high, relatedness seems to be less relevant explaining variation in sentinel behaviour (Duncan et al., 2019; Griffin and West, 2003), and other direct benefits seem to play a more important role. Variation in contribution to sentinel behaviour across species includes younger individuals acting as sentinels less than older individuals (Clutton-Brock et al., 2002; Ferguson, 1987; Rasa, 1977), while within age classes heavier individuals display more sentinel behaviour than lighter individuals (Bell et al., 2010; Clutton-Brock et al., 1999b; Wright et al., 2001b; Wright et al., 2001c). These results support the 'state-dependency hypothesis' (Bednekoff, 1997, 2001), demonstrating that sentinel behaviour, as a form of cooperation within the foraging and predation avoidance trade-off, is highly condition dependent. Although condition dependence can explain a large part of the variation found in sentinel behaviour there is evidence that yet additional benefits to the sentinel may play an important role. In birds dominant individuals show more sentinel behaviour than subordinates (Hollen et al., 2011b; Wright et al., 2001b) supporting

the 'social display hypothesis' that sentinel behaviour has evolved as a dominance display, whereby individuals benefit from being seen as sentinel (a sign of high quality and social prestige), ultimately resulting in sexually selected, direct benefits (Zahavi, 1989; Zahavi, 1990; Zahavi and Zahavi, 1999). Studies on dwarf mongoose (*Helogale parvula*) reported mixed results about whether dominant or subordinate individuals contribute more to sentinel behaviour (Kern et al., 2016; Rasa, 1987a). Because males generally show more sentinel behaviour than females (Clutton-Brock et al., 2002; Wright et al., 2001b), 'the information acquisition hypothesis' states that sentinel behaviour is used to collect information about the location of other groups or females to increase extra group mating opportunities or prospect dispersal opportunities (Clutton-Brock et al., 2002).

In this study, we assess the evidence for the social display and the information acquisition hypothesis, in addition to the known state-dependency hypothesis in the sentinel system of meerkats (*Suricata suricatta*). Meerkats are a small, highly cooperative mongoose species that occur in arid, semi-desert areas of southern Africa and live in groups from three to 50 individuals (Clutton-Brock et al., 1999a; Clutton-Brock and Manser, 2016; Doolan and Macdonald, 1996). Each group consists of a dominant, reproductive pair and helpers, which help to rear the dominant pair`s offspring by providing them with food and protection (Clutton-Brock et al., 1998b). This social system results in groups consisting mostly of full siblings (littermates) and half siblings (Clutton-Brock and Manser, 2016). During foraging meerkats dig holes in the sand in search for insects and small vertebrates (Doolan and Macdonald, 1996), which prevents them from scanning their surroundings for predators. Since meerkats forage in open environments, predation risks are high and individuals commonly alternate between foraging and acting as sentinels. While on guard, sentinels produce distinct sentinel calls informing the rest of the group about their presence (Manser, 1999) as well as their perceived predation risk (Rauber and Manser, 2017). In case the sentinel spots a predator, they produce functionally referential alarm calls containing information about the predator type as well as the urgency level (Manser et al., 2001; Manser et al., 2002).

We tested the non-mutually exclusive hypotheses about the underlying motivation of sentinel behaviour by quantifying the influence of social and ecological factors on the contribution to sentinel behaviour across individuals at different life history stages, within and between groups and populations, using a much larger dataset than in previous studies (Clutton-Brock et al., 1999b; Clutton-Brock et al., 2002). We analysed data collected over the past 23 years on sentinel behaviour and the related life history information of 1692 individuals from 53 groups to investigate the role of social factors. By comparing this data to a second population inhabiting an area with much higher predation pressure, where data from 63 individuals from 6 groups has

been collected over a period of two years, we also investigated the effect of predation risk on individual variation in sentinel behaviour including any interactions with social factors.

METHODS

Study sites and populations

Data for this study were collected at the Kalahari Meerkat Project (KMP) on two populations of wild, habituated meerkats. To analyse the effects of social factors on sentinel behaviour we used data collected between 1996 and 2019 at the Kuruman River Reserve in the southern Kalahari Desert, Northern Cape, South Africa (for more information about habitat at the study site, see Clutton-Brock et al. 1999; Russell et al.2002). This area (hereafter 'farm') has been used for farming and all large and medium sized terrestrial predators have been removed, resulting in low predation pressure. In total we used data on sentinel behaviour from 1692 individuals from 53 groups from this site. For the investigation of the effect of predation risk on sentinel behaviour, data from a second population, collected between 1993 and 1996 at the Kalahari Gemsbok National Park, also known as Kgalagadi Transfrontier Park, were added. From this site (hereafter 'park'), we used data from 63 individuals from 6 different groups. Both study sites consisted of similar, semi-arid habitat, however, predation risk at the park was much higher compared to the farm (total number of predators per 100 hours of observations: park 20.29±11.24; farm 4.49±6.38), resulting in significantly different mortality rates (Clutton-Brock et al., 1999a). In both sites all groups were habituated to close human observations allowing the recording of natural behaviours.

Sentinel behaviour and related life history information

Data about sentinel behaviour had been continuously collected at the KMP as part of the daily data collection. When an individual climbed on an elevated position (minimum height 10cm higher than the surroundings) and started actively scanning the area, its individual identity, group identity and the duration of the sentinel bout were recorded, as well as the overall observation time a group was observed on that day. We then calculated the mean monthly sentinel contribution per hour observed for every individual, resulting in a sample size of 22110 monthly values for the farm population and 502 monthly values for the park population. The main reason to work with monthly means rather than daily values was because not every animal acted as sentinel every day and to reduce potential short-term environmental influences like current

weather conditions. All related information including age, sex, dominance status and group size was available from the long-term data of the KMP and monthly means were calculated where applicable. For the analysis of the farm data we used all groups (ranging from 3 to 46 adults, mean = 17), however, to facilitate comparison between the two populations we only used groups with group sizes that occurred in both populations (3-25 adult individuals, mean (park) = 14) for the comparative analysis. We grouped individuals into the following age categories: subadults (6 to 12 months), yearlings (>12 to 24 months), adults (>2 to 4 years) and old adults (>4 years). Taking into account the well supported 'state dependency hypothesis', we used mean monthly morning weight, collected in the morning at the burrow before the group starts foraging, as a measure of condition. As meerkats show high competition among members of the same litter (Huchard et al., 2016), we tested for possible effects of competition on sentinel behaviour (as part of the "social display hypothesis") by examining the influence of same-aged, same-sexed littermates on an individual's contribution to sentinel behaviour. Inter-group interactions (IGIs) represent a costly behaviour and can thus be used to test condition dependence. Alternatively, they may also provide males with information about females in the area, therefore potentially being relevant for the 'information acquisition hypothesis'. To investigate how IGIs affect contribution to sentinel behaviour we calculated the number of IGI events a group had in each month (Drewe et al., 2009). To further assess the evidence for the 'information acquisition hypothesis' in males we calculated the number of days a male was temporarily absent from the group, assuming the male went roving (prospecting for mating opportunities with extra group females) (Young et al., 2005; Young et al., 2007), as well as the mean number of days between the month of interest and the day when the male permanently left the group (dispersal date). For females we calculated the number of days a female was absent from the group due to eviction by the dominant female (Clutton-Brock et al., 1998b; Clutton-Brock et al., 1998c; Stephens et al., 2004).

Statistical analysis

All analyses in this study were done using R version 3.5.2 (R Core Team, 2018). To investigate the effect of social and environmental factors on the contribution to sentinel behaviour we used linear mixed effects models (LMM, lem4 package (Bates et al., 2014)) with mean monthly sentinel duration per hour observed as response variable and individual ID nested in group ID is as well as a combined year-month variable as random factors. To investigate the variation in sentinel behaviour in females, we included the following fixed effects: age category; mean monthly morning weight; mean monthly group size including all adults >12 months; number of same-aged, same-sexed littermates; dominance status; number of days the female was evicted per month; number of monthly inter-group interactions (IGIs). For males we added number of days the male

went roving per month, immigration status (natal or immigrant) and the number of days until they permanently left their natal group (dispersal date).

To compare sentinel behaviour between the two populations we combined data from the farm and the park. Again, mean monthly sentinel duration controlled for observation time was used as response variable and predation risk, group size (ranging between 3-25 adults), the interaction between predation risk and group size, age category, sex, weight and dominance status were used as fixed effects. We tested for any interactions between population and the other fixed effects by comparing the model with the interaction to the same model without the interaction term, whereby non-significant interactions were excluded from the final model. To determine the fit of the linear mixed models, we examined the model diagnostic plots and response variables were log transformed to ensure the model assumption were met (Crawley, 2012).

Ethical note

All the observational data collection and weight measures within the course of this study fall under the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC031-13) and were carried out adhering to the approved guidelines in this permit.

RESULTS

Social factors influencing sentinel behaviour

The duration of sentinel behaviour shown per hour observed varied widely between individuals. In both, males and females, individuals between one and four years contributed more than subadults and adults over 4 years (Table 1). Mean monthly morning weight, our proxy for condition, significantly affected sentinel behaviour of males and females, whereby within each age class heavier individuals acted as sentinels more than lighter individuals. The interaction between age class and condition was the strongest in subadults and with increasing age heavier individuals contributed relatively less than lighter individuals (Table 1, Figure 1). With increasing group size both sexes reduced their individual sentinel behaviour (Table 1). However, with increasing number of same-aged female littermates, but not male littermates present in the group, females increased their contribution to sentinel behaviour (Table 1, Figure 2). In contrast, males generally increased their sentinel behaviour with increasing number of same-aged littermates (Table 1, Figure 2). In females, subordinates contributed more than dominants, but did not change their sentinel behaviour in response to the number of days they were evicted or the frequency of IGIs

per month (Table 1). In contrast, natal males showed higher contributions to sentinel behaviour than immigrants, while there was no difference in sentinel behaviour between dominant and subordinate males (Table 1). We found no significant interaction between dominance and immigration state. Males performed less sentinel behaviour with increasing roving frequency and IGIs (Table 1, Figure 3). Furthermore, we found that the closer males got to their dispersal date, the less they contributed to sentinel behaviour (Table 1).

Ecological factors influencing sentinel behaviour

When controlling for age, sex, group size and condition, meerkats from the park population – where predation risk was much higher - showed significantly more sentinel behaviour than the farm population with low predation (Table 2, Figure 4). Moreover, small groups showed much larger individual contributions in the park compared to the farm and an increase in group size in the park led to a larger decrease in sentinel behaviour than on the farm (Tale 2, Figure 5). We did not find any significant interactions between any of the other social factors, including sex, dominance state and immigration state with population.

Table 1: Social factors influencing monthly contribution to sentinel behaviour for males and females separately.

	Estimate ±Std. Error	df	t value	p
Females (Number of obs = 9339):				
(Intercept)	-0.705 ± 0.144	6188.47	-4.89	<0.001
Age Category (yearling)	**0.340 ± 0.034**	**8648.45**	**10.08**	**<0.001**
Age Category (2-4yrs)	**0.286 ± 0.046**	**7559.08**	**6.15**	**<0.001**
Age Category(>4yrs)	**0.154 ± 0.071**	**8313.65**	**2.18**	**0.029**
Morning Weight	**0.993 ±0.104**	**6933.02**	**9.53**	**<0.001**
Morning Weight:yearling	**-1.786 ± 0.210**	**9212.52**	**-8.49**	**<0.001**
Morning Weight:2-4yrs	**-2.258 ± 0.234**	**9192.76**	**-9.63**	**<0.001**
Morning Weight:>4yrs	**-2.631 ± 0.293**	**9056.99**	**-8.95**	**<0.001**
Group Size	**-0.202 ± 0.039**	**3216.71**	**-5.12**	**<0.001**
Nr. Female Littermates	**0.144 ± 0.018**	**4448.17**	**7.99**	**<0.001**
Nr. Male Littermates	**-0006 ± 0.028**	**1460.00**	**-0.22**	**0.830**
Dom State (sub)	**0.387 ± 0.053**	**5692.75**	**7.34**	**<0.001**
Nr. Evicted Days	-0.020 ±0.011	9040.70	-1.81	0.076
Nr. Monthly IGIs	0.020 ±0.012	7473.49	1.59	0.486

Males (number of obs = 12771):

(Intercept)	-1.803 ± 0.114	4211.78	-15.73	<0.001
Age Category (yearling)	**0.303 ± 0.031**	**6544.25**	**10.05**	**<0.001**
Age Category (2-4yrs)	**0.249 ± 0.042**	**6368.99**	**5.90**	**<0.001**
Age Category (>4yrs)	0.091 ± 0.065	6065.66	1.39	0.166
Mean Morning Weight	**2.128 ± 0.105**	**6339.39**	**20.28**	**<0.001**
Morning Weight:yearling	**-1.258 ± 0.278**	**6565.67**	**-4.52**	**<0.001**
Morning Weight:2-4yrs	**-2.263 ± 0.316**	**6347.29**	**-7.12**	**<0.001**
Morning Weight:>4yrs	**-1.783 ± 0.596**	**6458.24**	**-2.98**	**0.002**
Group Size	**-0.206 ± 0.037**	**2571.22**	**-5.49**	**<0.001**
Nr. Male Littermates	**0.046 ± 0.022**	**3145.68**	**3.38**	**0.048**
Nr. Female Littermates	**0.056 ± 0.021**	**4446.65**	**2.54**	**0.012**
Dom State (sub)	0.052 ± 0.059	2784.26	0.87	0.385
Imm State (natal)	**0.490 ± 0.086**	**2681.68**	**5.67**	**<0.001**
Dom State*Imm State	0.072 ± 0.085	4747.99	0.84	0.401
Roving Frequency	**-0.064 ± 0.010**	**6321.91**	**-6.31**	**<0.001**
Time to dispersal	**0.094 ± 0.031**	**1492.58**	**2.96**	**0.003**
Nr. Monthly IGIs	**-0.073 ± 0.011**	**4672.45**	**-6.57**	**<0.001**

Table 2: Effect of predation risk (farm vs park) and group size on the daily proportion of different individuals in a group contributing to sentinel behaviour.

	Estimate ±Std. Error	df	t value	p
(Intercept)	-1.416 ± 0.112	8927	-12.87	<0.001
Population (park)	**0.782 ±0.186**	**3622**	**4.21**	**<0.001**
Groupsize	**-0.009 ± 0.002**	**9634**	**-4.92**	**<0.001**
Pop (park)*Groupsize	**-0.037 ± 0.012**	**3225**	**-2.96**	**0.003**

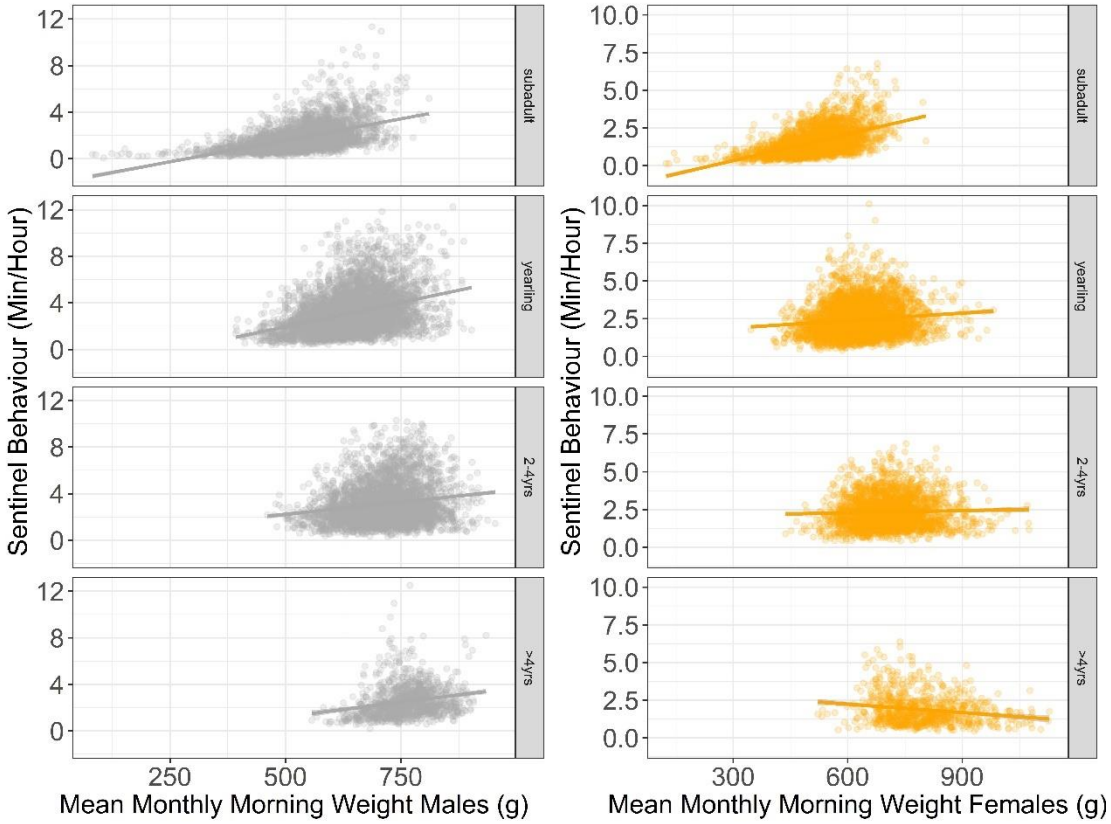

Figure 1. Age-dependent effect of mean monthly morning weight (condition) on monthly contribution to sentinel behaviour for males (grey) and females (orange).

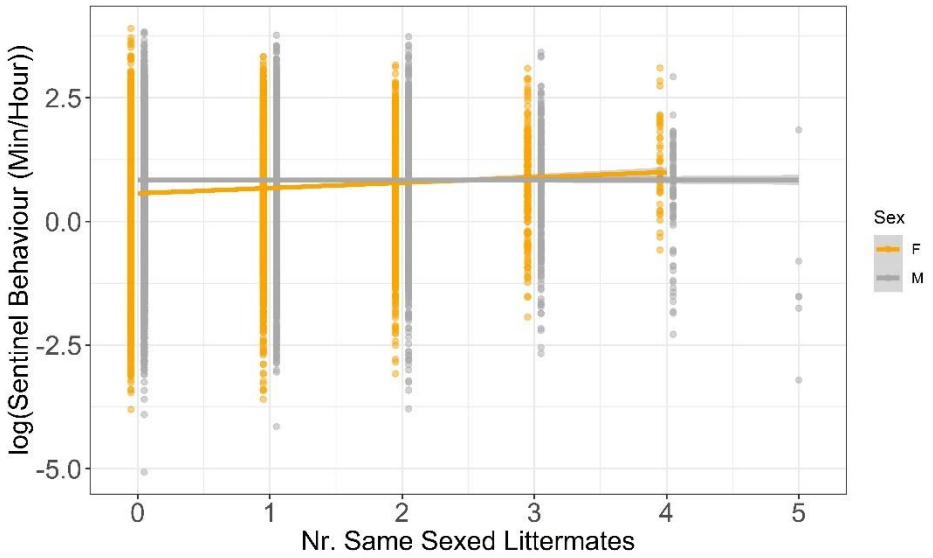

Figure 2. Effect of the number of same sexed, same aged littermates (usually full siblings) on monthly sentinel behaviour in males (grey) and females (orange).

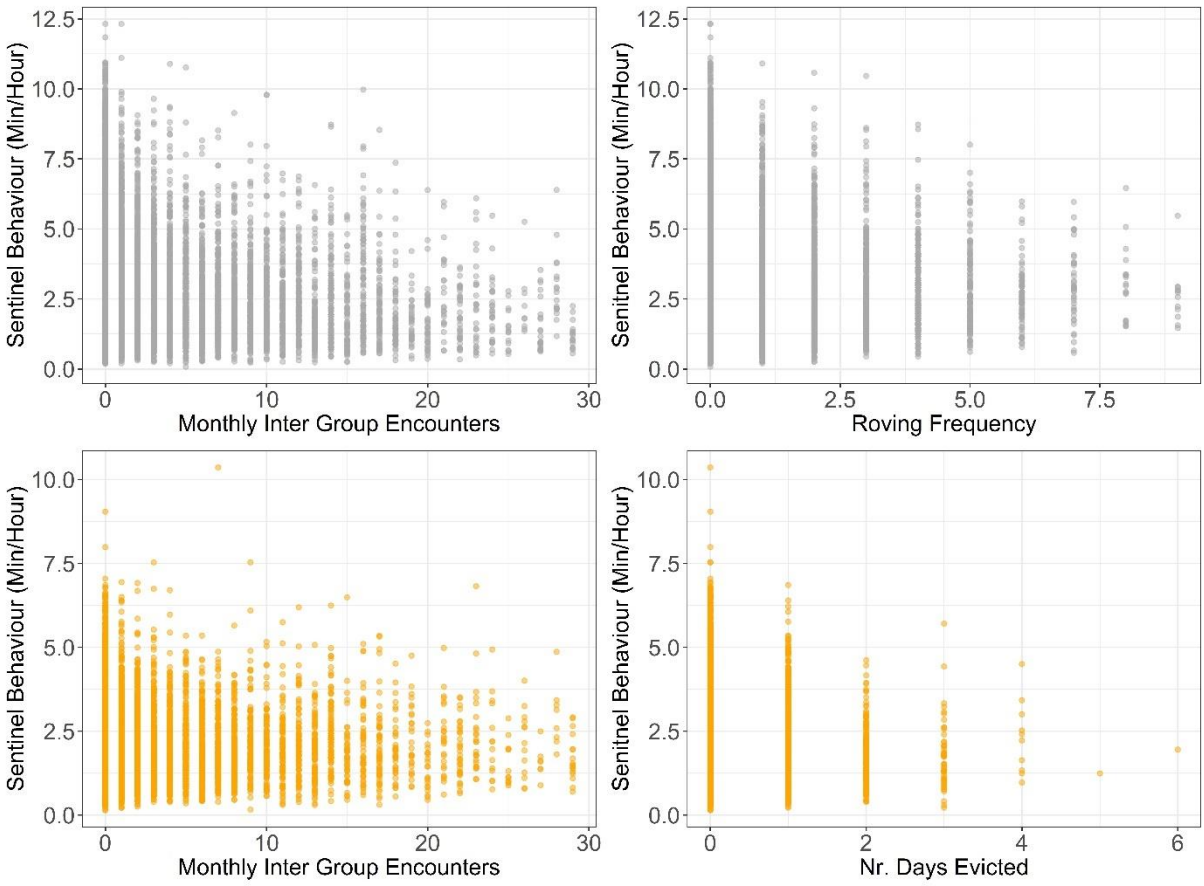

Figure 3. Effect of the number of monthly inter group encounters, roving frequency (for males) and number of days evicted from the group (for females) on monthly sentinel contribution in males (grey) and females (orange).

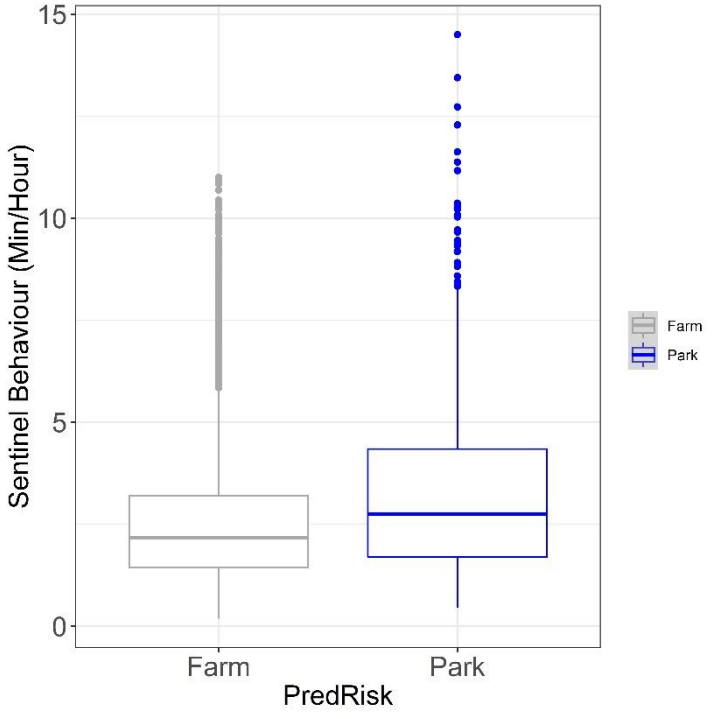

Figure 4. Comparison of individual monthly sentinel duration per hour observed between the two study populations. On the farm all large and medium sized terrestrial predators were removed, thus representing a low risk environment, while in the park predation risk was much higher.

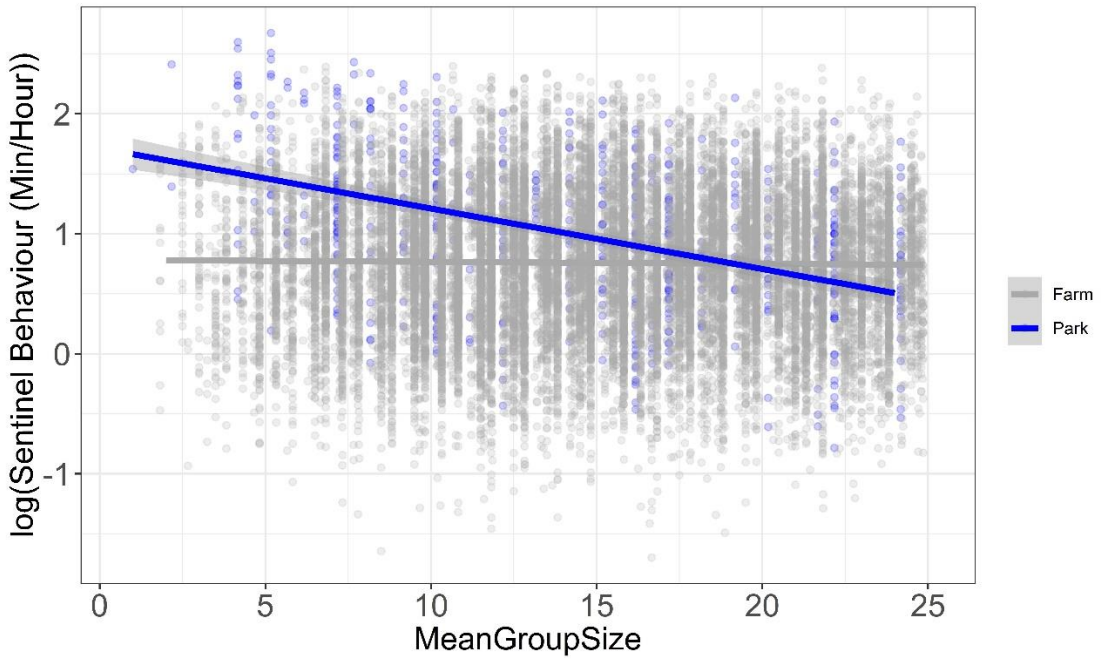

Figure 5. Effect of group size on individual contribution to sentinel behaviour in the park (high predation risk) and the farm (low predation risk).

DISCUSSION

Investigating the large individual differences in contribution to sentinel behaviour in meerkats, our results demonstrate that both sexes showed more sentinel behaviour with increasing body weight, however this effect decreased with increasing age. Furthermore, with increasing group size, each individual on average spent less time acting as sentinel guard, however, with increasing number of same-sexed, same-aged littermates, females (and to a lesser extent males), increased their contribution to sentinel behaviour. In females, dominants did less sentinel behaviour than subordinates, while time periods of evictions or intergroup interactions did not affect sentinel behaviour. In contrast, natal males generally displayed more sentinel behaviour than immigrants, but there was no difference between dominants and subordinates. Roving and intergroup interactions led to a decrease in sentinel behaviour in males, and the closer they got to their dispersal the less they contributed to sentinel behaviour. Individuals from an area with high predation risk (park) showed increased sentinel contributions, especially in small groups, and the decrease in sentinel contribution with increasing group size was larger in the park (high predation risk) than on the farm (low predation risk).

Individual condition had a major influence on meerkat sentinel behaviour, providing further support of the 'state dependency hypothesis' (Bednekoff, 1997; Bednekoff and

Woolfenden, 2003; Bell et al., 2010; Clutton-Brock et al., 1999b; Wright et al., 2001b). Within each age category, heavier individuals, which may be better foragers, spent more time as sentinel. This effect was stronger in younger age categories and less pronounced in older individuals, which might reflect an adjustment from helping towards gaining more direct benefits. This shift from investing in cooperative behaviours towards direct benefits is generally reflected by the fact that the contribution to most cooperative activities in meerkats peaks around two years of age and tends to decline in older individuals (Clutton-Brock and Manser, 2016). Older subordinates are more likely to disperse (Clutton-Brock et al., 2001a) and especially older males invest more time into prospecting behaviour in other groups (roving) (Mares et al., 2014). Increasing group size lightened the workload for each group member, resulting in lower individual contributions to sentinel behaviour, as shown for other cooperative behaviours in meerkats (Clutton-Brock et al., 2002).

In contrast to the overall group size effect, our results indicate that, especially in females, increasing number of same-aged female littermates, but not their male littermates, led to higher contribution to sentinel behaviour. This result may indicate that meerkats use sentinel behaviour as a dominance display among same-sexed, female litter members, potentially supporting the "social display hypothesis" (Zahavi, 1990; Zahavi and Zahavi, 1999). The fact that this seems to be stronger in females than in males and that there is no effect of number of male littermates on females is likely due to stronger competition among females, as they are the philopatric sex, and thus compete for the reproductive position in their natal group (Hodge et al., 2008; Young et al., 2006). Moreover, as condition seems to be a main determinant of who becomes the next dominant, when a previous dominant dies, we find the highest competition levels among same-aged females from the same litter (Hodge et al., 2008; Huchard et al., 2016). However, the role of sentinel behaviour as a dominance display in intrasexual competition, indicating potentially better quality or competitive abilities, likely based on higher foraging success resulting in higher satiation, remains unclear. In Arabian babblers (*Turdoides squamiceps)* (Dattner 2015) and white-browed sparrow weaver (*Plocepasser mahali*), dominant males profit from acting as sentinels by facilitating the defence of paternity and dominance status against extra-group males (Dattner et al., 2015; Walker et al., 2016). However, as others (Wright et al., 2001a; Wright et al., 2001c) have found no evidence of the role of social display in sentinel behaviour, more research is needed to assess the influence of competition on sentinel behaviour.

In males, we provide new evidence that when additional costly situations occurred, such as encounters with other groups, or when a male temporary left the group to prospect for mating or dispersal opportunities (Young et al., 2005; Young et al., 2007), sentinel contribution decreased. This is likely explained by the elevated stress levels related to these behaviours as well as the decreased amount of time available for foraging, which often lead to a decrease in body weight (Young et al., 2005; Young et al., 2006). In contrast to previous work (Clutton-Brock et al.,

1999b), we show here that when males got closer to their dispersal date, they performed less sentinel behaviour. Males may invest in maximizing their weight, which is key factor in gaining dominance in a new group, or in a coalition of males. In support of this hypothesis recent work on dominant males has shown that individuals that are heavier at dispersal are more likely to gain dominance in the future (Spence-Jones et al, in prep). Overall, the decreased sentinel behaviour relative to IGIs, roving frequency and dispersal time contradict the previously introduced "information gathering hypothesis" (suggesting that males may be looking out for other groups and potential mating opportunities) but support the idea that sentinel behaviour is highly state dependent.

Besides the social environment, our results confirm previous work demonstrating an increased individual sentinel contribution in areas of higher predation risk (park). Moreover, in areas of higher predation risk, increasing group size led to a stronger decrease in sentinel behaviour, indicating larger constraints in animals in the park population, and thus the importance of group size benefits under these conditions. Although other variables such as vegetation density or structure might also differ between the two populations and could have influenced sentinel behaviour, it is likely that the large difference in predation pressure resulted in the found differences in contribution. This supports previous work demonstrating the effect of ecological factors influencing perceived risk on individual contributions to sentinel behaviour (Hollen et al., 2011b; Ridley et al., 2010).

We conclude that sentinel behaviour is the mutualistic outcome of a finely balanced trade-off between benefits of maximizing foraging time for the sentinel as well as the whole group and the costs of being exposed to predators. Therefore, our results support previous work that sentinel behaviour is highly state-dependent. However, we provide new evidence that sentinel behaviour may also be used as a dominance or social display when competition among individuals of the same sex is high, though this seems only come into play under specific conditions, with specific group structure. In contrast, we found no indication that sentinel behaviour is related to increased prospecting or dispersal behaviour shown by males in order to gain information about the presence of females. Thus, by testing the effect of social and ecological variables on individual contribution to sentinel behaviour, we provide further insights into the causal and functional mechanisms controlling cooperation in social mammals.

AUTHORS' CONTRIBUTIONS

RR and THCB were involved in planning the study. RR conducted the data extraction and statistical analyses. RR wrote the first draft and MBM and THCB equally contributed to the subsequent revision of the manuscript. THCB and MM organised the long-term data collection at the KMP on cooperative behaviour, weights and life history data.

COMPETING INTERESTS

We declare we have no competing interests.

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CHAPTER 2

2. DROUGHT DECREASES COOPERATIVE SENTINEL BEHAVIOUR AND AFFECTS VOCAL COORDINATION IN MEERKATS

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ABSTRACT

Cooperative breeding often evolved in harsh and arid habitats characterised by high levels of environmental uncertainty. Most forms of cooperative behaviour have energetic costs and previous studies have shown that the contributions of individuals to alloparental provisioning are conditional on the food intake of individuals. However, the effect of naturally occurring, extreme environmental conditions on the persistence of costly forms of cooperative behaviours and their coordination by communication remain unknown. Here, we show that in meerkats (*Suricata suricatta*) the probability to act as sentinel, a cooperative vigilance behaviour, was the same for typically occurring dry and wet conditions, but significantly reduced during a drought condition

with almost no rain, especially in young individuals, members of small groups and groups with pups. The duration an individual stayed on sentinel guard, however, was most reduced during dry conditions. Besides reductions in sentinel behaviour, the vocal coordination of foraging meerkats differed when comparing drought and wet conditions. Individuals responded more strongly to playbacks of sentinel 'all-clear' calls and close calls, resulting in less vigilance and more foraging behaviour during the drought condition. We conclude that while meerkats are adapted to commonly occurring dry periods with low rainfall, the extreme drought period with almost no rain, led to a decrease of the frequency of costly forms of cooperative behaviours in favour of behaviours that maximize direct fitness benefits and also affect the vocal coordination among group members.

Key words: drought, cooperative breeders, sentinel behaviour, sentinel calls, acoustic communication

INTRODUCTION

Both in birds (Jetz and Rubenstein, 2011) and mammals (Lukas and Clutton-Brock, 2017), cooperative breeding systems, where individuals forego their own independent reproduction while helping others in the group to rear their young, are commonly associated with environments where resources are scarce. In many of these environments, rainfall and temperature vary widely within and between years (Jetz and Rubenstein, 2011; Lukas and Clutton-Brock, 2017), generating unpredictable fluctuations in resource availability that are commonly associated with variation in breeding success and survival (Clutton-Brock et al., 1999a; Dai, 2011). A recent study on cooperatively breeding birds showed a decrease in cooperative provisioning of young by adult group members during days with unusually high temperatures (Wiley and Ridley, 2016) and previous studies of meerkats (*Suricata suricatta*) have provided experimental evidence that cooperative behaviours are conditional on foraging success and are reduced when daily weight gain of animals is low (Clutton-Brock et al., 2001b; Clutton-Brock et al., 1999b). Together, these results suggest that cooperative breeders need to adjust their investment in cooperative behaviours in relation to variation in weather conditions as well as in food availability, especially in response to extreme events, such as droughts, defined as prolonged periods with rainfall significantly below the level received in commonly occurring dry years (Botai et al., 2016). Currently, the effect of naturally occurring, extreme environmental conditions, including reduced food availability, on the persistence of cooperative behaviours has not been explored.

It has been suggested that cooperative breeders may have evolved a more complex communicative system than less social species in order to coordinate group living and cooperative activities (Freeberg et al., 2012; Leighton, 2017; Manser et al., 2014). It is well known that social factors, such as sex, life history stages, or dominance status, influence the behavioural responses to vocal signals (Fischer et al., 2004; Mitani and Brandt, 1994; Snowdon and Elowson, 1999) but the extent to which extreme environmental conditions affect vocal coordination remains unclear. For example, warning or alert calls that are not associated with an immediate threat but rather with a general increase in perceived predation risk or uncertainty might be more likely to be ignored during adverse environmental conditions when individuals need to maximize foraging in order to survive. Thus, drought conditions might affect the behavioural responses of individuals to specific vocal signals and the coordination of cooperative behaviour.

In this study, we investigated potential differences in cooperative sentinel behaviour and its vocal coordination in meerkats between a year of drought, three years of dry conditions and three years of wet conditions (Table 1). Meerkats forage in small groups from 3 to 50 individuals composed of different age classes (pups < 3 months, juveniles 4-6 months, subadults 7-12 months, yearlings 13-24 months and adults > 24 months) (Clutton-Brock et al., 1999a; Clutton-Brock et al., 2006). Each group consists of a dominant, reproductive pair and subordinates, which help to rear the dominant pair`s offspring by providing them with food and protection (Clutton-Brock et al., 1998b). Meerkats have an elaborate sentinel system where one individual is on raised guard at an elevated location, scanning the surroundings for the presence of predators and alerting the group in case of danger (Clutton-Brock et al., 1999b). Besides alarm calls elicited in response to an approaching predator (Manser, 2001; Manser et al., 2001), sentinels also produce functionally specific sentinel calls, which inform the rest of the group about the guard`s temporary perceived predation risk and lead to the adjustment of vigilance behaviours by foraging group members (Manser, 1999; Rauber and Manser, 2017). Sentinel calls include calming calls, which have an 'all clear' function and lead to an increase in foraging and a decrease in vigilance behaviour in receivers, and warning calls, which decrease foraging and increase vigilance behaviour for the rest of the group (Rauber and Manser, 2017).

Contributions to sentinel behaviour reduce foraging opportunities. The costs of foregoing foraging are likely to increase under adverse environmental conditions, leading to stronger trade-offs between cooperative behaviours and individual survival. Average rainfall in our study area in the Southern Kalahari since 2009 has been 98 mm between December and January but due to the severe El Nino event in 2015/16 rainfall was less than 1 mm during the same time period and the weight and breeding success of resident animals was reduced ((Wiley and Ridley, 2016); unpublished data long-term database). To test whether and how drought conditions affected cooperative behaviours, we measured the contributions of individuals to sentinel behaviour

during a year of drought, three dry years of low rain conditions and three wet years of high rain conditions (Table 1). In particular, we investigated the effects of drought on the probability to act as a sentinel and the duration of guarding periods. We predicted that while meerkats should be adapted to dry years, drought conditions increase the costs of cooperative behaviours. As a consequence, we expected to find that animals reduce both the probability that individuals would go on sentinel guard and the duration of sentinel bouts in order to increase foraging time and thus individual survival. We expected this effect to be most pronounced in younger individuals and members of small groups, whose foraging success is relatively low (Clutton-Brock et al., 1999b; English et al., 2014). Furthermore, we expected drought to decrease the skew in guarding contribution within groups as single individuals might not be able to maintain higher sentinel frequencies compared to the rest of the group. In regards to vocal coordination, we investigated the consequences of drought on the responses of individuals to sentinel warning and calming calls, using a series of playback experiments. We predicted that under drought conditions foraging meerkats respond stronger to sentinel calming calls ('all-clear' function) and reduce their response to sentinel warning calls (pre-stages of alarm calls) to increase foraging efficiency in comparison to non-drought conditions (Rauber and Manser, 2017).

METHODS

Study site and species

Data were collected at the Kalahari Meerkat Project (KMP) located at the Kuruman River Reserve in the southern Kalahari Desert, Northern Cape, South Africa (for more information about habitat at the study site see Clutton-Brock et al., 1999; Russell et al., 2002). The climate at the study site is characterised by two distinct seasons: a cold-dry season from May to September (mean monthly rainfall 5.5ml) and a hot-wet season from October to April (mean monthly rainfall 45.7ml) (Clutton-Brock et al., 1999; Russell et al., 2002). As part of the KMP's long-term data collection, all group members were uniquely dye marked to allow individual recognition, and one or two individuals of each group were fitted with radio-collars to facilitate localisation of the group (Jordan et al., 2007). All groups were habituated to close human observations and to the playback equipment, allowing us to perform recordings and playbacks within a distance of 0.5 m to the test subjects.

Analysis of long-term data

Individual sentinel events and their durations were collected between December and January from 2009 to 2016 by volunteers of the Kalahari Meerkat Project as part of the daily long-term data collection. We assigned each period of these seven years to one of three environmental conditions – wet, dry and drought – based on the amount of rainfall measured directly at the study site during the middle of the wet season, which includes the months December and January. To account for any carry-over effects from previous rainfalls, we also added the amount of rainfall during the three months before the analysed periods, i.e. September to November. This resulted in the following categorisation: 2009/2010, 2010/2011 and 2011/2012 represented wet years, 2012/2013, 2013/2014 and 2014/2015 were dry years, and 2015/2016 was a drought year with almost no rain between December and January (Table 1). A sentinel event always consisted of an individual climbing on an elevated position of at least 10cm above ground and actively scanning the environment (Clutton-Brock et al., 1999b). To investigate whether the different environmental conditions affected the probability of individuals to go on guard we included every individual (total n = 750; n = 266 adults, n = 504 yearlings, n = 370 subadults, n = 193 juveniles, due to the multi-year data structure some individuals appear in several age categories) from every group (n = 26) in the analysis and checked whether each of these individuals acted as sentinel or not for each observation day (n = 28773 observations). This resulted in a daily yes/no response variable for every group member present on the day of data collection. Following this, we compared observed daily sentinel durations by calculating the total time individuals were on sentinel guard during the 3.2 ± 0.02 hours of observations per day (including morning and evening sessions) resulting in a total of 3969 sentinel events of 480 different individuals (n = 179 adults, 312 yearlings, 180 subadults, 21 juveniles, due to the multi-year data structure some individuals appear in several age categories). All individuals' age, sex, dominance status, group size, and whether and how many pups were in the group were documented. We investigated the effect of any interaction between environmental condition and age, sex, dominance status, group size, presence of pups and number of pups on the observed time (min) individuals spent on sentinel duty per day.

Table 1. Environmental conditions based on rainfall measured at study site.

Year	Rainfall (ml) December-January (study period)	Rainfall (ml) September-November	Total amount of rain (ml) September - January	Environmental Condition (EC)
2009/2010	178.0	NA	178.0*	Wet
2010/2011	195.2	28.6	223.8	Wet
2011/2012	116.4	1.0	117.4	Wet
2012/2013	16.6	15.4	32.0	Dry
2013/2014	57.4	5.8	63.2	Dry
2014/2015	24.6	16.4	41.0	Dry
2015/2016	0.6	11.6	12.2	Drought

*minimum estimate due to lack of rain data at study site before December 2009

Sound recordings

Sound recordings for the playbacks of the different sentinel call types were collected in May 2014 prior to the start of the first playback experiments. Calls from naturally occurring sentinel events were recorded using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling frequency 44.2 kHz, 16 bits accuracy). A Rainhardt microphone windshield (W200) was permanently attached to the microphone to ensure high quality recordings in the meerkats' natural environment. The microphone was fixed to a telescopic pole in order to maintain a recording distance of less than 0.5 meters and a high signal-to-background ratio.

Playback experiments

In order to compare behavioural responses to sentinel vocalisations during a non-drought and a drought condition we repeated the same series of playbacks we had done for previous work (Rauber and Manser, 2017) in the non-drought period from June to August 2014 in the drought period of 2015/2016 from January to the 8th of March 2016. The rainfall measurements for these

two periods differed substantially in regards to the amount of rain in the 3 months period before and the 3 months period of the playback experiments, with the non-drought period having received 112ml and the drought period 15.2ml over the total of 6 months. When testing the probability to act as sentinel, this was significantly higher during the non-drought period compared to the drought period (GLMM; $\beta \pm se = 1.32 \pm 0.39$, $z = 3.41$, $p < 0.001$), indicating that, besides any other potential seasonal differences, environmental conditions were less constraining for meerkats during the non-drought period. We conducted playback experiments in a total of 12 groups with group size of three to 24 individuals. Following the same protocol as previous work on the behavioural response to sentinel vocalisations (Rauber and Manser, 2017), we selected single calls with a high signal-to-noise ratio using Cool Edit Pro (Syntrillium Software Corporation) to compose playback files consisting of sentinel calls and close calls (control) from the same individual. Close calls are soft, close range contact calls that are frequently emitted during foraging and used for group coordination (Fichtel and Manser, 2010; Gall and Manser, 2017).

Sentinel calls of recordings from at least six different and independent recording events from the same individual (n=8) were used for each playback file. The calls from at least three different individuals were played back to each group, using a Marantz PMD-670 solid-state recorder, connected to a portable speaker (iHome IHM79SC). The amplitude was assessed according to how the calls occur under similar natural weather and wind conditions. The call rate of the specific sentinel calls and close calls was kept the same as observed in natural recordings (close calls: 8.25 ± 2.28 calls/min; single note calls: 3.79 ± 0.43 calls/min; double note calls: 3.19 ± 0.37 calls/min) with background noise between each call (Rauber and Manser, 2017). For the sentinel warning calls context we always played a total of four calls, two “di-drrr” and two “wheek” calls in alternating order and with at least one minute of background noise in between, which also lies in the range of natural recordings (di-drrr: 0.34 ± 0.12 calls/min; wheek calls: 0.39 ± 0.09 calls/min Rauber and Manser, 2017). Playback experiments were only conducted when no predator had been seen for at least 15 minutes and only if the majority of the group was foraging undisturbed for at least five minutes. If any of the conditions, including the absence of predators, were violated after the playback had been started, the playback was paused and resumed only after the majority of the group was back to normal foraging behaviour for a minimum of five minutes or the sentinel finished its guarding session. We played back a series of six five-minutes sound files to an adult foraging meerkat, resulting in playbacks of a length of 30 minutes each. The full playback consisted of five minutes of the two different sentinel call types (i.e. calming and warning calls), five minutes of close calls (cc) in the beginning, between the two types of sentinel calls and afterwards and also five minutes of background noise (bkg) either at the very beginning or the end (e.g. cc-calming-cc-warning-cc-bkg). During the playbacks each behaviour of the test

subjects was recorded as a focal follow using the program Cybertracker (Cybertracker Conservation 2013 version 3.376) on a handheld tablet (Acer IconiaOne 7 B1–750). Four adult individuals (>12 months, the dominant pair and one subordinate of each sex) of eight groups were tested to playbacks, resulting in a sample size of 32 playbacks for each year. To keep the playback procedure the same as in 2014, when we were also interested in the potential difference between calls from the same versus from another group, half of the playbacks were from individuals from the same group and the other half from individuals from another group.

Analysis of behavioural focals

Behavioural responses to sentinel calls are of short duration and are only obvious within the first 30 seconds after the playback of a call (Rauber and Manser, 2017). Therefore, to analyse the response of the test subjects we calculated the proportion of time the meerkats spent foraging and being vigilant during the first 30 seconds after four randomly (sample function of the R base package) chosen calls of each of the different playback contexts (close calls, calming sentinel calls, warning sentinel calls). As each playback file consisted of three identical copies of five-minute tracks of close calls the proportions of time spent for each behaviour was averaged for the analysis (here after called average cc). For the background noise context we chose four random time points and analysed the behaviour in the following 30 seconds. As foraging behaviour, we grouped foraging (digging in a hole for prey), scrabbling (head down while scratching at multiple small holes or surface), processing (processing food items in sand, or chewing off tail of scorpions, etc.) and eating. Regarding the alert-related behaviours, we focused on two types of vigilance behaviour: quadrupedal (head up while scanning the sky and the surroundings on all four legs) and bipedal (scanning of sky and surroundings standing on the hind legs with upright body position).

Statistical analysis

All analyses in this study were done using R version 3.2.0 (R Core Team, 2018). To determine the relationship between sentinel behaviour and the different parameters we conducted linear mixed effects models (LMM) and generalized linear mixed effects models (GLMM), depending on whether the data met the assumptions of normality and homogeneity of variance (Bates et al., 2014). To determine the fit of linear mixed models we examined the model diagnostic plots and response variables were transformed where assumptions of the models were not met (Crawley, 2012) . Post-hoc multiple comparison tests with manually set contrasts were done whenever the

predictor variable consisted of more than two categories to compare the different categories not specified by the intercept (Hothorn et al., 2008).

To analyse the effect of environmental conditions on an individual's observed daily probability to go on guard, we fitted a generalized linear mixed effects model with guarding (0/1) as response variable, thus, using binomial distribution. Because there was no significant difference of guarding between wet and dry years while they were both significantly different from the drought year we pooled those together as 'non-drought years' to facilitate model convergence. Age class, sex, dominance status, group size, presence of pups and number of pups were each tested as interaction with drought as fixed effects and individual ID nested in group ID and observation date were added as random effects.

To investigate the effect of environmental conditions on sentinel duration we fitted a LMM with individual sentinel guarding time per observation day as response variable and again age class, sex, dominance status, group size and presence of pups were each tested separately as interaction with drought as fixed effects. individual ID nested in group ID were added as random effects. To determine whether sentinel duties were more evenly distributed within the group during the drought compared to wet and dry years we calculated the proportion of different sentinel individuals as the number of all individuals acting as sentinel per observation day divided by the total group size (not including pups which don't contribute to sentinel behaviour (Hollen et al., 2008b)). We then used the log-transformed proportion of sentinels as response variable in a LMM with environmental conditions, group size and the interaction between drought and group size as fixed effects and group ID as random factor. Since there was again no difference between dry and wet years while both being significantly different from drought, we pooled these two conditions together as non-drought period to improve model convergence. Lastly, to analyse the effect of environmental conditions on the response to sentinel calls (playback experiments) and the two different control conditions (close calls and background noise), we conducted generalized mixed models with the proportion of the behaviour of interest (number of seconds out of the total 30 seconds after a call) as response variable using the cbind function and family binomial (Crawley, 2012). Individual ID was nested in group ID as random factors. The three behaviours of interest were foraging, quadrupedal vigilance and bipedal vigilance. Whenever the explanatory variable consisted of more than two categories multiple comparison test with manually set contrasts (glht function of multcomp package) were used to compare the different categories not specified by the intercept, or to compare specific contrasts (Hothorn et al., 2008). The p-values were generated using adjusted p-values using Bonferroni correction (Hothorn et al., 2008).

Ethical note

All the experiments and recordings conducted within the course of this study fall under the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC031-13) and were carried out adhering to the approved guidelines in this permit.

RESULTS

Effect of environmental conditions on probability that individuals act as sentinel

While there was no difference in the probability that individuals acted as sentinels during wet and dry years ($\beta = 0.13 \pm 0.23$, $z = 0.55$, $p = 0.583$), meerkats went on sentinel guard significantly less during the drought condition compared to the dry ($\beta = -1.01 \pm 0.32$, $z = -3.18$, $p = 0.001$) and wet conditions ($\beta = -0.89 \pm 0.33$, $z = -2.67$, $p = 0.007$). Therefore, wet and dry conditions were pooled together as 'non-drought' conditions and then compared to the drought condition. During the drought condition, we found that, juveniles and subadults reduced the frequency of them acting as sentinel significantly more than adults (Table 2; Figure 1a). The same decrease was observed with yearlings, however, less strong. This reduction in sentinel frequency was stronger in smaller groups and in groups where pups were present (Table 2; Figure 1a, b). There was no interaction between environmental conditions and either dominance status or sex on the likelihood to show sentinel behaviour.

Effect of environmental conditions on sentinel duration

The dry condition had a negative effect on the duration to stay on sentinel guard compared to wet conditions ($\beta = -0.11 \pm 0.03$, $t = -3.5$, $p < 0.001$; Figure 2). The drought condition was not significantly different from dry ($\beta = 0.04 \pm 0.05$, $t = 0.84$, $p = 0.403$; Figure 2) or wet ($\beta = -0.06 \pm 0.05$, $t = -1.03$, $p = 0.304$; Figure 2) conditions. None of the tested variables including age class, sex, dominance status, group size and presence of pups showed a significant interaction with the three environmental conditions (wet, dry and drought).

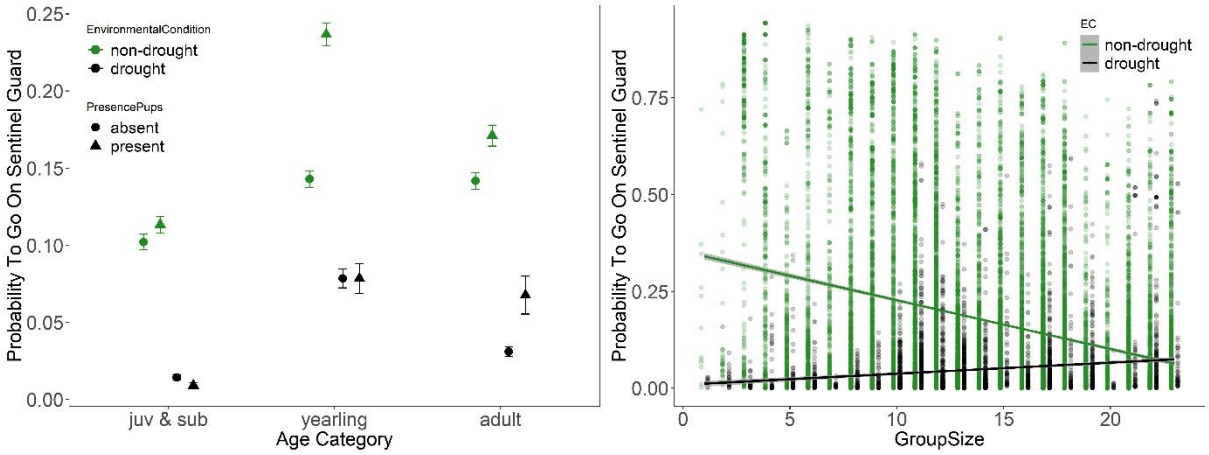

Figure 1. Model estimates of the daily probability to go on sentinel guard during drought (black) and non-drought (green; wet and dry conditions pooled together as they were statistically not different) for a) the different age classes and whether there were pups present in the group or not and b) different group sizes. Shown are estimates for subordinates only, which did not differ from dominant individuals.

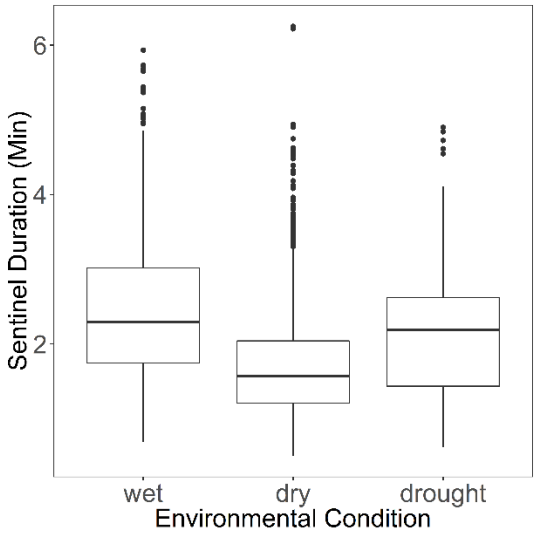

Figure 2. Boxplots of average predicted duration of a single sentinel event (in min) during each of the three environmental conditions (wet, dry, drought). The bold horizontal line represents the median while the box shows the interquartile range between the 25% and 75% percent quartiles. Whisker show data range of 1.5 times the interquartile range from the 25% and the 75% quartiles.

Table 2. GLMM model output investigating the interactions between environmental condition (EC) and sex, age class, dominance status, group size, presence and number of pups on observed daily sentinel probability (Number of obs=28773, groups: Code:Group=901; WatchDate= 210; Group=35).

Fixed Effect	Effect±SE	Df	X^2	P
(Intercept)	-2.54±0.26			
Environmental condition (EC)	**-1.92**±0.52	**1**	**54.20**	**<0.001**
Age Category (Juv and Sub)	**-0.79**±0.10			**<0.001**
Age Category (Yearling)	**0.44**±0.08			**<0.001**
Sex(M)	**0.48**±0.11			**<0.001**
Dom Status (Sub)	0.11±0.12			0.329
Group Size	**-1.49±0.13**			**<0.001**
Presence Pups	**0.59±0.05**			**<0.001**
EC:Age Class		**3**	**22.27**	**<0.001**
EC:Juv and Sub	**-1.00±0.39**			**0.012**
EC:Yearling	**-0.59±0.27**			**0.026**
EC:Group Size	**1.68±0.53**	**1**		**0.002**
EC:Presence Pups	**-0.83±0.27**	**1**	**2.71**	**0.002**
Random effects	**Var**	**sd**		
Code:Group	**1.61**	**1.27**		
Watch Date	**1.91**	**1.38**		

Significant variables are shown in bold.

Effect of environmental conditions on distribution of sentinel duties among group members

The proportion of individuals contributing to sentinel behaviour within a group was significantly lower during the drought compared to the dry (β = -0.06±0.02, t = -3.04, p = 0.003) and the wet (β = -0.05±0.02, t = -2.16, p = 0.031) conditions. Dry and wet conditions did not differ (β = 0.01±0.01, t = 1.16, p = 0.247), thus were pooled together to non-drought conditions. There was an interaction between environmental conditions and group size such that, for small groups during drought conditions, the proportion of individuals contributing to sentinel behaviour was the same or slightly higher than during non-drought conditions, while the opposite was true for larger groups. They showed significantly lower proportions of sentinels during the drought (Table 3; Figure 3). Follow up analyses excluding very small groups of less than six individuals, as well as very large groups of more than 22 individuals, confirmed the robustness of this result.

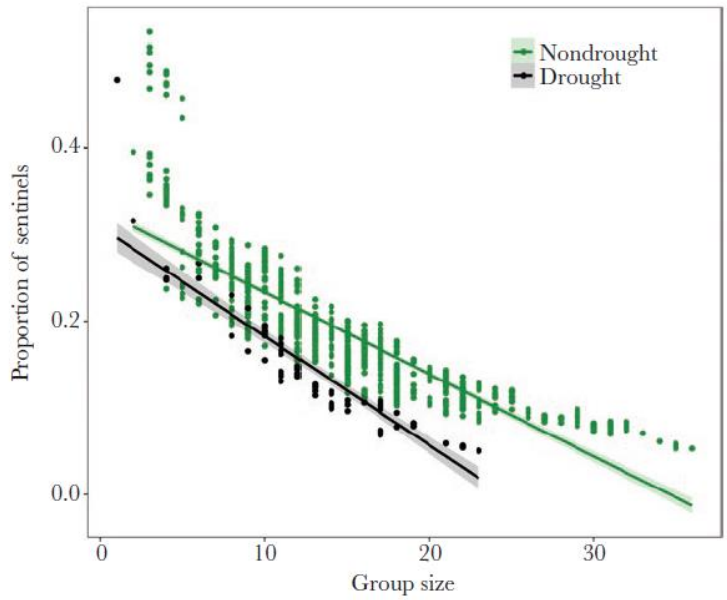

Figure 3. Relationship between predicted daily proportions of individuals in a group that acted as sentinels during drought (black) and non-drought periods (green; wet and dry conditions pooled together as they were statistically not different).

Table 3. Main effects and interaction of environmental condition (EC) and group size on the proportion of different sentinels within a group (as determined by a linear mixed model; Number of obs= 883, groups: Watch Date= 175; Group=25).

Fixed Effect	Estimate± SE	Df	X^2	P
(Intercept)	-0.99±0.07			
Environmental Condition (EC)	0.20±0.21	1	35.65	0.335
Group Size	-0.05±0.01	1	215.25	**<0.001**
EC:Group Size	-0.04±0.01	1	0.99	**0.003**
Random effects	**Var**	**sd**		
Group	**0.04**	**0.21**		
Watch Date	**0.01**	**0.09**		

Significant variables are shown in bold.

Effects of environmental conditions on response to sentinel calls

Foraging meerkats responded differently to the four tested playback conditions during the drought in comparison to the non-drought period. The playback of sentinel calming calls elicited less bipedal vigilance in the drought compared to the non-drought period (Table 4; Figure 4c). Close calls (average cc), on the other hand, led to more foraging behaviour during the drought (Table 4; Figure 4a), while background noise tended ($p < 0.1$) to elicit less foraging behaviour (Table 4, Figure 4a) and more quadrupedal vigilance behaviour (Table 4; Figure 4b) during the drought period. We did not, however, find any evidence, that warning sentinel calls were more likely to be ignored during the drought period (Table 4; Figure 4c).

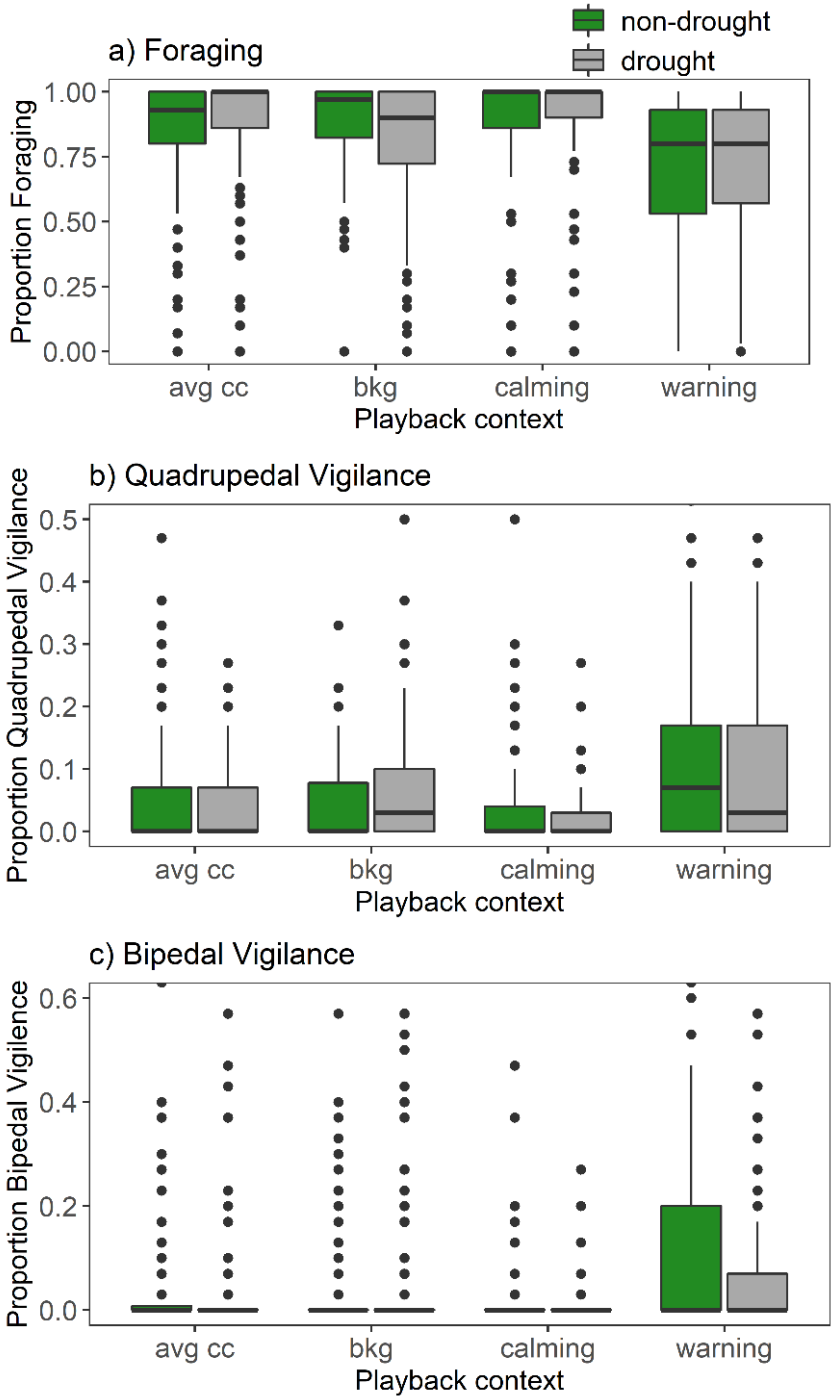

Figure 4. Comparison of (a) foraging, (b) quadrupedal vigilance and (c) bipedal vigilance behaviour given in response to the four different playback conditions (close calls (= average cc), background noise (bkg), calming sentinel calls, warning sentinel calls) between drought and non-drought period.

Table 4. GLMM model output and post-hoc multiple comparison test to compare foraging, quadrupedal vigilance and bipedal vigilance during the different playback conditions between drought and non-drought year (Number of obs = 946, number of playbacks = 60, Code:Group = 56, Group = 12).

Behaviour	Condition	Estimate± SE	z-value	*P*
Foraging	(Intercept)	2.88 ± 0.30		
	Close calls	**0.84 ± 0.41**	**2.04**	**0.04**
	Background	-0.70 ± 0.41	-1.73	0.08
	Calming	0.49 ± 0.43	1.12	0.26
	Warning	0.04 ± 0.39	0.09	0.93
Quadrupedal	(Intercept)	-4.13 ± 0.28		
Vigilance	Close calls	-0.22 ± 0.33	-1.42	0.15
	Background	**0.71 ± 0.32**	**2.45**	**0.01**
	Calming	-0.08 ± 0.35	-0.29	0.77
	Warning	-0.11 ± 0.31	-0.65	0.52
Bipedal	(Intercept)	-3.11 ± 0.27		
Vigilance	Close calls	-0.62 ± 0.37	-0.67	0.09
	Background	-0.42 ± 0.37	-1.12	0.26
	Calming	**-1.02 ± 0.38**	**2.67**	**0.007**
	Warning	-0.17 ± 0.36	0.48	0.63

Significant variables are shown in bold.

DISCUSSION

Our results show the frequency of cooperative behaviours in meerkats to be significantly reduced during naturally occurring, extreme environmental conditions with limited food availability, supporting previous work on food dependency of cooperative behaviours. While the probability of cooperative sentinel behaviour was the same during commonly occurring dry and wet years, in the extreme drought year with almost no rain, a shift in the investment from cooperative behaviours to foraging behaviour with immediate individual benefits was observed, and vocal group coordination was also affected. During the drought year, individual meerkats reduced the frequency with which they contributed to sentinel behaviour. These reductions were largest in young individuals of less than two years, members of smaller groups, and in groups with pups. Compared to smaller groups, in larger groups the contribution to sentinel behaviour was less evenly distributed among group members during the drought compared to the non-drought (dry and wet years taken together) periods. Meerkats also responded more strongly to calming sentinel calls and contact calls, showing more foraging and less vigilance behaviour in the drought year than in a year with wet conditions. Background noise, however, led to less foraging and more vigilance behaviour in the drought year.

In accordance with our predictions, we found that within groups, especially young individuals, i.e. juveniles and subadults, were less likely to act as sentinel during the drought. Yearlings (1-2 years old) also showed less sentinel behaviour during the drought compared to adults, however, the effect was less strong than in the younger age class. Furthermore, we found that group size and composition significantly affected the probability to act as sentinel when comparing the drought year with the dry and wet years. Members of small groups and groups with pups reduced the sentinel frequency during the drought more than members of larger groups and groups without dependent offspring. The effect of group size is likely explained by the higher individual contribution to sentinel behaviour in smaller groups (Clutton-Brock et al., 1999b). The found effect of presence of pups suggests that having dependent offspring (pups) comes with additional costs of helping behaviours such as allolactation, pup feeding and protection of pups (Clutton-Brock and Manser, 2016). As the survival of young is critically dependent on provisioning from adults, it is not surprising that these behaviours are prioritized over sentinel behaviour as a response to limited resources.

Duration of sentinel behaviour per guarding event was longest during wet years. A likely explanation is that during these conditions vegetation is usually much taller and denser compared to dry years and the drought year and meerkats need to stay on sentinel guard longer in order to scan the area for the presence of predators, in particular terrestrial predators. In addition, there is more food available in the wet season leading to individuals being faster satiated and thus able

to afford to be on sentinel guard for longer periods of time. Against our predictions, we did not find a difference in sentinel duration between the dry years and the drought year. The reduction in sentinel duration in dry years may be due to the fact that compared to the drought year meerkats still keep up the same frequency of sentinel behaviour during dry years as during wet years when food is plentiful. Therefore, when conditions get harder there seems to be a trade-off between frequency of cooperative behaviours and duration. During dry years it seems that mainly duration was reduced while during the drought year it was mainly the frequency that decreased with which individuals maintain cooperative behaviours. Further research is needed to explore this relationship in other cooperative behaviours, in particular using more drought years.

In terms of how sentinel behaviour is distributed among group members, we provide evidence that larger groups showed a bigger decrease in the number of different individuals going on sentinel guard per day in the drought, while the proportion of individuals acting as sentinel of smaller groups stayed the same as in non-drought years. Together with the effect of group size on the probability to act as sentinel, this suggests that in smaller groups, the same number of animals go on shorter sentinel bouts, while in larger groups fewer animals act as sentinels in the drought, but those can afford to keep the total time the group has a sentinel similar to non-drought years. Thus, larger groups were able to maintain cooperative behaviours, while cooperative behaviours in smaller groups were significantly reduced in the drought year. This is in line with previous work that shows the benefits of living in larger groups due to lower individual contribution to cooperative behaviours (Clutton-Brock et al., 1999b).

Not only investment into sentinel behaviour changed depending on environmental conditions, but also the vocal coordination of foraging meerkats. Test subjects responded more strongly to playbacks of sentinel calming calls, which act as 'all-clear' signal, resulting in less vigilance and more foraging behaviour in the drought period in comparison to the non-drought period. A likely explanation is that during demanding conditions individuals rely more on 'all-clear' signals in order to maximize foraging. We did not, however, find any evidence that meerkats were more likely to ignore sentinel warning calls in the drought period compared to the non-drought period. This is in line with work on alarm calls, where the costs of not responding to calls related to predators have been suggested to be too high to ignore (Schibler and Manser, 2007). The fact that meerkats were more vigilant during the drought when they heard background noise may indicate, that as a consequence of the decrease in cooperative vigilance behaviour, individuals experience higher levels of uncertainty in perceived predation risk and thus invest more time into personal vigilance behaviours. Additionally, hearing no calls from other group members might increase the perceived risk of losing the group (Gall and Manser, 2017), due to meerkats being more spread out when food is spatially and temporally more scattered (Rymer et al., 2016). This is supported by findings that during drought conditions foraging meerkat groups

split more often compared to dry conditions (Gall, 2017) and can also explain our result that meerkats were less vigilant when they heard contact calls during the drought, indicating close proximity to other group members (Gall and Manser, 2017). However, other differences in seasonal related factors, e.g. spatial cohesion or foraging time, between the two playback periods, besides the amount of rain and sentinel frequency, cannot be excluded to have impacted the behavioural response of foraging meerkats to sentinel calls. Further playbacks are needed to confirm the importance of specific environmental factors on a species' communication system.

In conclusion, our results suggest that naturally occurring, extreme environmental conditions, such as droughts, decrease the contribution to cooperative behaviours, as shown on the sentinel behaviour in meerkats. Furthermore, these reductions in frequency and to a lesser extent duration of cooperative vigilance behaviour were associated with changes in the vocal coordination of foraging meerkats. Although meerkats, and cooperative breeders in general, are adapted to arid, unpredictable environments (for example Cockburn and Russell, 2011; Schneider and Kappeler, 2014), extreme environmental conditions that reduce food availability affect the investment of individuals in cooperative activities and the vocal coordination of cooperative behaviours. Therefore, we argue that there is likely an ecological threshold beyond which some aspects of cooperation including cooperative vigilance behaviour and provisioning of young (Wiley and Ridley, 2016) seem to collapse. Our study offers new insights about how extreme environmental conditions influence the occurrence of cooperative behaviours and the consequences for group coordination in cooperative breeders.

AUTHORS' CONTRIBUTIONS

RR and MBM were involved in planning the study. RR conducted the experiments and statistical analyses. RR, MBM and THCB equally contributed to the writing of the manuscript. THCB and MM organised the long-term data collection at the KMP on cooperative behaviour, weights and life history data.

COMPETING INTERESTS

We declare we have no competing interests.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by (Rauber et al., 2019ahttps://doi.org/10.5061/dryad.1s73fc5).

CHAPTER 3

3. EFFECT OF GROUP SIZE AND EXPERIENCE ON THE ONTOGENY OF SENTINEL CALLING BEHAVIOUR IN MEERKATS

R. Rauber & M. B. Manser

ABSTRACT

Increased vulnerability to predation and a larger set of predators result in young individuals of many species experiencing higher predation pressure. Consequently, antipredator-related calls produced by young individuals can differ from the same vocalisations given by adults. Sentinel behaviour is a coordinated vigilance behaviour, where one individual climbs on an elevated position and scans the surroundings for predators, while the rest of the group is mainly foraging. Meerkat sentinels produce six distinct sentinel call types, which inform the rest of the group about the perceived predation risk, resulting in the adjustment of personal vigilance behaviour in foraging group members. In this study we investigated the onset of sentinel behaviour and the ontogeny of the different sentinel call types as well as the development of individual vocal signature in young meerkats. Our results demonstrate that meerkats started acting as a sentinel

guard around 200 days of age, but this was highly dependent on group size, with individuals from smaller groups exhibiting sentinel behaviour earlier than individuals from larger groups. All six types of sentinel calls were already present in the repertoire upon first emergence of the behaviour, however, call rates of 'all-clear' sentinel calls increased while warning sentinel calls decreased with increasing experience as sentinel. Analysis of one of the most common calming sentinel calls, the double note calls, indicated that fundamental frequency, mean amplitude, duration and entropy differed consistently between individuals (i.e. different extent and rates of change), but we found no effect of age. Lastly, our results provide evidence that individual signatures of young meerkats were already developed when they first started to go on sentinel guard and changed little in subsequent months. To conclude, we show that sentinel behaviour as well as its vocal coordination undergo very little ontogenetic changes before reaching maturity, indicating potentially high selection pressures on antipredator behaviours, such as the sentinel system, resulting in consistent behavioural response upon first emergence.

Keywords: ontogeny, sentinel behaviour, acoustic communication, individual vocal signature

INTRODUCTION

As a consequence of living in groups, some animals have evolved specific coordinated antipredator defence mechanisms (Krause and Ruxton, 2002; Kruuk, 1964; Zoratto et al., 2009), such as sentinel behaviour (Horrocks and Hunte, 1986; Manser, 1999; McGowan and Woolfenden, 1989). Sentinel behaviour is a coordinated vigilance behaviour mostly seen in cooperative breeders, where one individual climbs on an elevated position and scans the surrounding for predators while the rest of the group is foraging (Bednekoff, 2015; Clutton-Brock et al., 1999b; Horrocks and Hunte, 1986; McGowan and Woolfenden, 1989; Ridley and Raihani, 2006; Wright et al., 2001a; Zahavi, 1990). Sentinels have been demonstrated to detect predators more frequently and from greater distances than foraging group members (Manser, 1999; Wright et al., 2001b) and foraging group members show a higher foraging efficiency when a sentinel is on guard (Hollen et al., 2008a; Manser, 1999).

When sentinels spot a predator, they produce specific alarm calls, allowing group members to initiate the proper antipredator behaviour (Bednekoff, 2001; Manser, 2001; Manser et al., 2001; McGowan and Woolfenden, 1989; Rasa, 1989). Alarm calls represent a common antipredator strategy (Caro, 2005; Sherman, 1977), and are thought to be under intense selection. However, selection pressures can vary between different group members, and are generally

higher for younger individuals than adults. Thus, offspring environment (Berg et al., 2013) as well as differences in predation risk due to higher vulnerability to predation in general or a different set of predators than adults, result in selection pressures that can be very different from those of adults. Consequently, alarm calls produced by young individuals have been demonstrated to differ from calls produced by adults on three levels: vocal production (i.e. the development of species-specific calls with correct acoustic properties), vocal usage (i.e. the correct choice of calls given the circumstances) and lastly development of the appropriate response to conspecific alarm calls (Hollen and Radford, 2009; Seyfarth and Cheney, 1986). In meerkats (*Suricata suricatta*), for example, it has been shown that young produce higher pitched and longer calls (Hollen and Manser, 2007), they call more often in response to non-threatening stimuli (Hollen et al., 2008b) and newly emerged young show stronger responses to alarm calls, which over the course of ontogeny become more and more adult-like (Hollen and Manser, 2006). Furthermore, studies on primates suggest a gradual acoustic ontogenetic development of some vocalisations, which may require exposure to specific acoustic stimuli as well as vocal practice, similar to what has been described in song birds (Seyfarth and Cheney, 1986). Thus, young individuals across many taxa undergo vocal ontogenetic development between birth and maturity.

Animals with individually distinct calls including some birds (Jouventin and Aubin, 2002; Lefevre et al., 2001; Radford and Ridley, 2008), primates (Cleveland and Snowdon, 1982; Miller and Thomas, 2012; Salmi et al., 2014; Snowdon and Cleveland, 1980), hyenas (Theis et al., 2007) and social mongooses (Jansen et al., 2012; Manser, 1999; Sharpe et al., 2013) provide another aspect of vocal ontogeny: the ontogenetic development of acoustic individuality. Individually distinct vocalisations reduce uncertainty levels in receivers, allowing them to adjust their behavioural response to the caller identity (Salmi et al., 2014). In the context of mother offspring behaviour, discrimination among individuals based on vocal signals provides the potential for reliable recognition of dependent offspring and therefore offspring survival, while avoiding misdirected maternal care (Briefer and McElligott, 2011b; Volodin et al., 2011). In the context of anti-predatory behaviours, group members of various species have been demonstrated to adjust the response to alarm calls depending on the identity of the caller (or some characteristics of the caller) and the associated quality and relevance of the provided information (Blumstein and Daniel, 2004; Blumstein et al., 2004; Hare and Atkins, 2001; Ramakrishnan and Coss, 2000). However, whether subadult individuals already possess individually distinctive calls when they first start producing the relevant call types, such as alarm calls, or whether this is something that develops during vocal ontogeny often remains unknown.

In addition to alarm calls, sentinels have been observed to produce the so called "Watchman's song", which allows foraging group members to obtain acoustic information about the presence of a sentinel individual (Hollen et al., 2008a; Manser, 1999; Rasa, 1986). The

structure and information content of sentinel vocalisations vary greatly, with some species producing one type of sentinel call to announce their presence, while others produce graded information contained in call rate of the sentinel call, which informs the rest of the group about changes in the perceived predation risk (Hollen et al., 2011a; Kern and Radford, 2013; Rauber and Manser, 2017). However, very little is known about the ontogeny of sentinel behaviour (Bednekoff, 2015), and nothing about the ontogeny of sentinel vocalisations. Thus, it remains unknown at what age the different sentinel calls are exhibited and whether and how sentinel calls produced by young differ from those produced by adults.

In this study we investigated the onset and vocal ontogeny of sentinel behaviour in young meerkats. Meerkats are small, highly sociable mongoose occurring in the Kalahari Desert in southern Africa (Clutton-Brock et al., 1999a; Clutton-Brock and Manser, 2016). They are cooperative breeders living in groups of three to 50 individuals (avg = 17), containing one dominant breeding pair and multiple subordinate helpers, which help to rear the dominant's offspring by providing them with food and protection (Clutton-Brock et al., 1998b; Clutton-Brock et al., 1999a; Clutton-Brock and Manser, 2016). Meerkats on sentinel duty produce six different sentinel call types and in case a predator is detected they give functionally referential alarm calls (Manser, 1999). The sentinel calming calls are produced when no predator is in sight and function as an 'all-clear' call, leading to an increase in foraging behaviour and a decrease in vigilance behaviour by the rest of the group (Rauber and Manser, 2017). Sentinel warning calls, on the other hand, are emitted when the sentinel individual experiences an increase in perceived risk and function as a pre-stage of alarm calls, leading to an increase in vigilance behaviour and a decrease in foraging by receivers (Rauber and Manser, 2017). In contrast, alarm calls contain information about different urgency levels of a flight response as well as information about the predator type, i.e. terrestrial or aerial (Manser, 2001; Manser et al., 2001; Manser et al., 2002). Having these varying levels of urgency in the same sentinel context, allows us to compare vocal ontogeny of sentinel calls with that of alarm calls regarding call usage, call production and development of individual signatures. Moreover, meerkat sentinel calls are individually distinct (Manser, 1999) and foraging group members adjust their behavioural response to sentinel calming calls based on the experience levels of the caller (Rauber and Manser, 2018).

First, we investigated at what age young individuals began to act as sentinels and whether and how group size influenced the onset of this behaviour. Individual contribution to sentinel behaviour decreases with increasing group size (Clutton-Brock et al., 1999b). Accordingly, young individuals in smaller groups might have to contribute more to this coordinated vigilance behaviour at a younger age in smaller groups, alternatively it is possible that in larger groups, which have on average more often an individual on raised guard (Clutton-Brock et al., 1999b), young individuals learn more quickly from other group members. Secondly, we determined the

age when different sentinel call types were first produced by young meerkats and how call rates changed until maturity. Based on the different urgency levels of sentinel calming and warning calls and due to the higher vulnerability of young individuals to predation we expected young individuals to produce more warning calls and less calming calls. Lastly, focusing on double note calls, one of the most common sentinel call type, we examined the amount of individuality encoded in this call and how it changed with increasing age of the signaller. As short note calls are also used in other context, it is possible that individuals that start going on guard have already developed their individually distinct call signature.

METHODS

Study site and population

This study was carried out between February and July 2017 at the Kalahari Meerkat Project (KMP) located at the Kuruman River Reserve in South Africa. Additionally, the analyses relied on long term data collected in previous years. The study site has a semi-arid climate and is characterised by perennial grasses, shrubs and trees as main vegetations (see Clutton-Brock et al., 1999a; Doolan and Macdonald, 1996; Doolan and Macdonald, 1997 for more information about the habitat and climate at the study site). All animals recorded during this study were habituated to close human observations and sound recording equipment, allowing for recording distances of less than 1m. Information about individual identity, age, as well as the frequency of sentinel behaviour was collected as part of the KMP's long-term data collection. In total, we used eight groups with group size varying between nine and 24 individuals (mean ± sd = 14.1 ± 6.25). Age classes were characterised as following: individuals younger than 3 months, i.e. pups, are for the most part dependent on feeding and protection from adult group members. Juveniles, 3-6 months, start to forage on their own, but still get complementary feeds from adults. Subadults, 6-12 months, forage independently and show more adult like behaviours, including offspring care or burrow maintenance. Individuals over 12 months of age are considered adults.

Behavioural data from the long-term database

We extracted the age at the first sentinel bout equal or longer than one minute for every meerkat born between August 2011 and October 2016, resulting in a total of 428 meerkats. One minute was chosen to exclude individuals that were just climbing up an object and were mistakenly noted down as sentinel individual. If the individuals stay in the raised position for a minute or longer, we can assume that this individual is acting as a sentinel and not just exploring its surroundings.

Acoustic recordings

We recorded a total of 191 sentinel events in eight groups (5-69 recordings per group; mean = 21) containing 1165 calls from 48 meerkats between 112 and 380 days old. Recordings were conducted during naturally occurring sentinel bouts using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling frequency 44.2 kHz, 16 bits accuracy). A windshield (Rainhardt, W200) was attached to the microphone to ensure high quality recordings under variable wind conditions. The microphone was attached to a 1.5m telescopic pole in order not to disturb the calling meerkats by keeping a distance of 1m between the meerkat and the recording person, while at the same time the recording distance was <0.5m and thus allowing for high signal-to-background ratio.

Extraction of acoustic parameters

Each vocalisation in the recordings was manually assigned to one of the six described sentinel call types and alarm calls (Fig.1) using a combination of visual inspection of the spectrogram and acoustic classification of calls in Adobe Audition (2015.0 Release)(Manser, 1999; Rauber and Manser, 2017). Work on previously described meerkat call combinations found that the silence interval between two combined calls is generally 20 times less than the silence interval among vocalisations that were considered to be independently produced (Collier et al., 2017). We used the same criteria here to categorise each of the six types of sentinel calls (Manser, 1999).

To extract acoustic parameters of one the most commonly produced sentinel call types, the double note call, we used Avisoft SASLab Pro (version 5.2.12). Upon loading the sound file into the program, we first removed noise levels below 250Hz applying a high-pass domain finite impulse response (FIR) filter. Afterwards we created spectrograms (FFT length = 512, overlap = 87%) and visually checked the tracking of the fundamental frequency (F0) and the duration of the elements. Calls that were not of high enough signal to noise quality and thus were not tracked correctly by the program were removed from the analysis. Similar to work by Salmi and collegues (2014) we only included individuals with at least four high quality calls. Additionally, we only used individuals where we had at least four independent recordings from different sentinel events. Fundamental frequency and peak amplitude were measured at 10 regular intervals throughout a call element but only measurements 2-9 were used for analysis as the first and the last were most imprecise and affected by background noise.

Statistical analysis

All statistical analyses were done using R Version 3.3.0 (R Core Team, 2018). To analyse the effect of group size on the age at first sentinel bout, we used a linear mixed model (LMM) with age (in days) as a response and sex and group size as fixed effect. Group identity was included as a random factor. As contribution to sentinel behaviour is higher in smaller groups, and because group size had a significant effect on the onset of sentinel behaviour, young individuals from smaller groups may acquire more experience sooner than individuals in larger groups. Hence, for further analysis of the ontogeny of sentinel vocalisations, we used the "GuardSum", which has been calculated as the total duration of all sentinel events of a given individual until the day of the recording. To test whether the presence of a given call type in the recordings was affected by age or experience, we used a generalized linear mixed model (GLMM) with the presence of a call type as binomial response variable and group size and age or guard sum respectively. Sentinel ID, group ID and date were used as random factors.

Following the methods used in Salmi et al. (2014), we compared the variation between calls of different individuals to the variation measured within individuals to assess whether calls show the potential for individual coding (PIC). To do this we measured the acoustic variability of each acoustic parameter (derived for each call element) by calculating the inter-individual variation means ($MEAN_{inter}$ = average mean of the measured parameter over the calls of all individuals) and the standard deviation (SD_{inter} = sd of the measured parameter over the calls of all individuals). Then we calculated the coefficients of variation between individuals (CV_{inter} = 100* $SD_{inter}/MEAN_{inter}$) and within individuals (CV_{intra} = mean of individual CV values; with CV=100*SD/MEAN for each individual). PIC was calculated as CV_{inter}/CV_{intra} , whereby values above 1 indicate higher variation between individuals than within individuals and thus the potential for this variable to encode individual information (Salmi et al., 2014). To test for any changes in individual distinctiveness across ontogeny, we used discriminant function analysis (DFA; Klecka and Iversen, 1980) on the measured acoustic variables of ten individuals younger than 250 days and ten individuals between 250 and 380 days of age to get the percentage of correct assignment of calls to individuals, using the leave-one-out method (Hair et al., 1995). For both age categories we used 16 calls per individual resulting in 160 calls each.

Ethics

All the recordings and observations used in this study were conducted with the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit Number: ECO31-13).

RESULTS

Starting age to act as sentinel

Mean age when meerkats first began to act as sentinel guard for a minute or longer was 196.9 ± 66.7 days (mean ± std. dev.). Young meerkats in larger groups had their first sentinel bout at a later age than meerkats in smaller groups (LRT: df = 1, χ^2 = 8.43, p = 0.004; LMM: β = 0.05, se = 0.01, p = 0.004). Males did not differ significantly from females in the age at first sentinel bout (LMM: β = -8.92, se = 6.51, p = 0.17). Because group size affected the onset of sentinel behaviour, the following analyses used relative individual experience (total guard sum), rather than absolute age, to investigate ontogenetic changes in sentinel call usage across individuals of different groups.

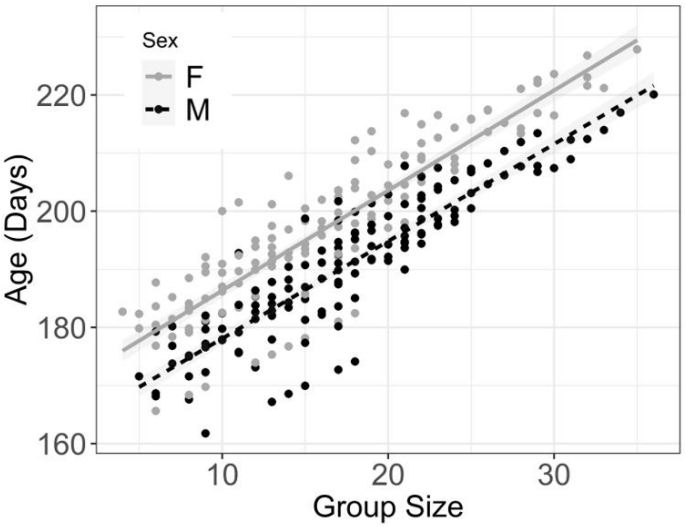

Figure 1. Influence of group size on age when females (grey) and males (black) were first recorded to act as sentinels for at least a minute.

Onset and use of the different sentinel call types

All six described sentinel call types were present in recordings of the youngest individuals (112-127 days old). Accordingly, the likelihood to find any of the six sentinel call types in a given recording was not affected by the sentinel experience (guard sum) of the individual on sentinel guard (Table 1; Fig.2). However, the call rates of some of the six different call types used during sentinel behaviour changed with experience of the calling individuals, i.e. how often the caller had acted as a sentinel before (Table 2). Single note calls significantly increased with increasing experience as sentinel, i.e. guard sum, whereby larger groups had shallower slopes than smaller groups (Table 2., Fig. 2). In contrast, the call rate of wheek calls decreased with increasing experience of the caller. Again, this effect was smaller in larger groups, meaning that smaller groups decreased the proportion of wheek calls faster than larger groups.

Table 1: Effect of sentinel experience (the total amount of time (GuardSum in minutes) an individual had been recorded as sentinel) on probability to produce each of the six described sentinel call types.

Call Type	Estimate	Std error	P value
Single note (sn)	0.32	0.34	0.336
Double note (dn)	0.38	0.38	0.32
Triple note (tn)	-0.11	0.27	0.701
Multiple note (mn)	0.84	0.44	0.078
Di-drrr call (didr)	-0.49	0.32	0.123
Wheek (wh)	-0.03	0.24	0.908

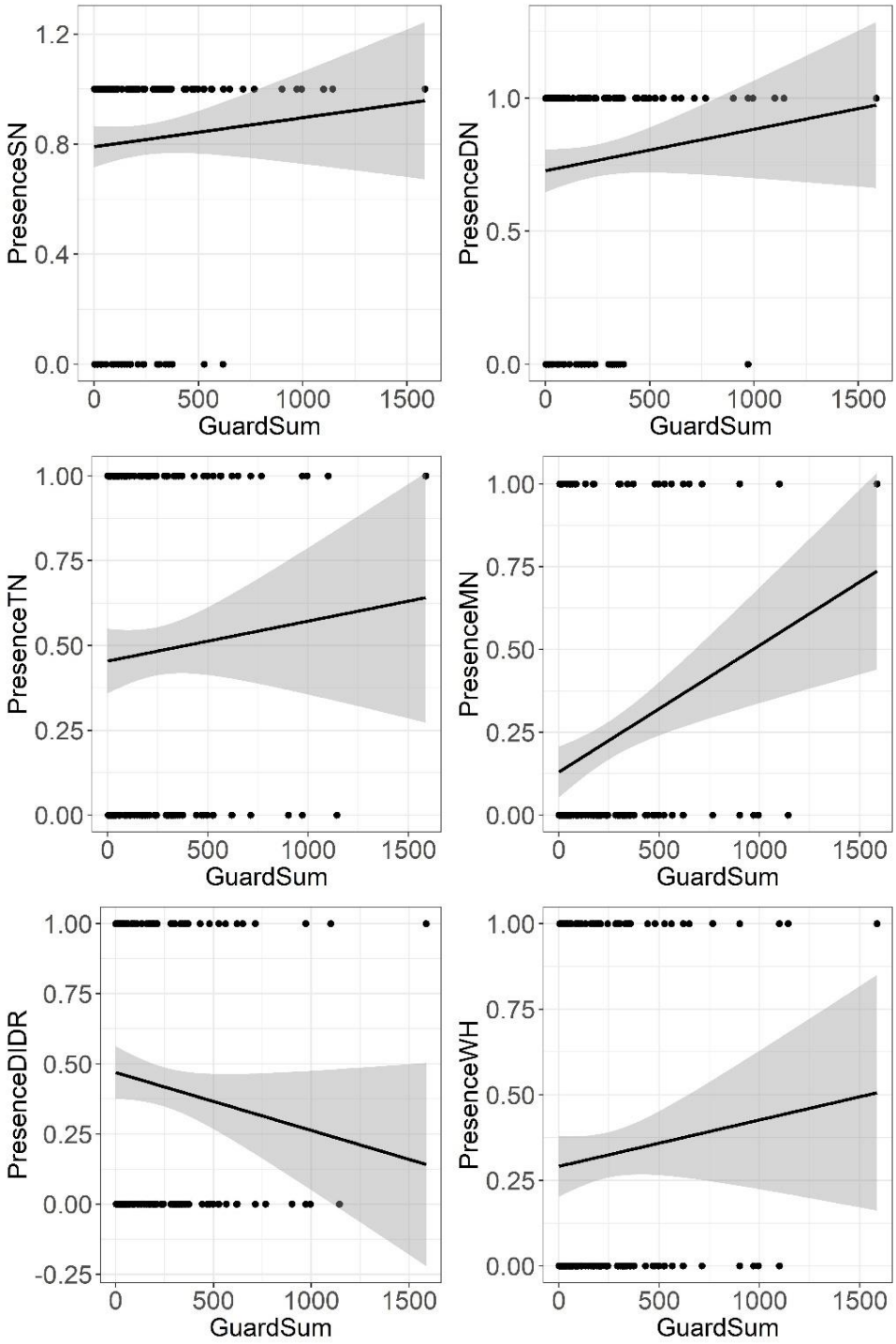

Figure 2. Appearance of each of the six sentinel call types in sentinel recordings of young meerkats between six and 15 months in relation to sentinel experience, i.e. the total amount of time (GuardSum in minutes) an individual has been recorded as sentinel.

Table 2: Effect of sentinel experience (the total amount of time (GuardSum in minutes) an individual has been recorded as sentinel) and group size on changes in call rate of the six described sentinel calls.

CallType	Variable	Est	Standard error	P
Sn	**Guard Sum**	**0.65**	**0.25**	**0.012**
	Group Size	0.31	0.28	0.183
	Guard Sum*Group Size	**-0.66**	**0.25**	**0.020**
dn	Guard Sum	-0.05	0.28	0.899
	Group Size	0.35	0.44	0.959
tn	Guard Sum	-0.24	0.24	0.148
	Group Size	-0.122	0.389	0.286
	Guard Sum*Group Size	0.228	0.235	0.052
Mn	Guard Sum	-0.101	0.24	0.670
	Group Size	0.57	0.56	0.330
Didr	Guard Sum	0.01	0.16	0.931
	Group Size	0.93	0.65	0.245
Wh	**Guard Sum**	**-1.583**	**0.65**	**0.018**
	Group Size	-0.329	0.66	0.620
	Guard Sum*Group Size	**1.81**	**0.62**	**0.008**

Ontogeny of acoustic parameters and individuality

Visual inspection of mean fundamental frequency (f0), mean peak amplitude (ampl), duration and mean entropy of the first element of the double note calls showed high variation in the amount (total difference between first and last recording) and degree of change (slopes) for different individuals over age (Fig.3). Accordingly, we found consistent individual differences in the mean of all measured parameters (different intercepts; LRT, f0: df = 1, $\chi^2 = 46.47$, $p < 0.001$; ampl: df = 1, $\chi^2 = 14.71$, $p < 0.001$; duration: df = 1, $\chi^2 = 63.09$, $p < 0.001$; entropy: df = 1, $\chi^2 = 8.90$, $p = 0.003$), but no general effect of age (Table 3). Due to the current data structure we were unable to test whether individuals also differed from each other across age (different slopes). The potential for individual coding (PIC) of all measured variables was above 1 (mean fundamental frequency: PIC = 1.46; mean peak amplitude: PIC = 1.46; duration: PIC=1.65; mean entropy: PIC = 1.22), thus all variables had the potential to be individually distinct. DFA analysis resulted in 65% correct assignment of ten individuals younger than 250 days, which was significantly higher than expected by chance (C.I. = 0.57-0.72, expected by chance = 0.1, $p < 0.001$). Call analysis of 10 individuals between 250 and 400 days showed a correct assignment of 57.7% (C.I. = 0.57-0.77, expected by chance = 0.1, $p < 0.001$), which suggests consistent individual distinctiveness when individuals first act as sentinels up to six months later.

Table 3. Effect of age on mean fundamental frequency, mean peak amplitude, duration and mean entropy of the first note produced in double note calls.

Acoustic parameter	est±se	t	p
Mean Fundamental Frequency	0.01±0.24	0.06	0.97
Mean Peak Amplitude	-0.02±0.01	-1.65	0.10
Duration	0.01±0.01	-0.766	0.447
Mean Entropy	-0.01±0.01	-1.25	0.217

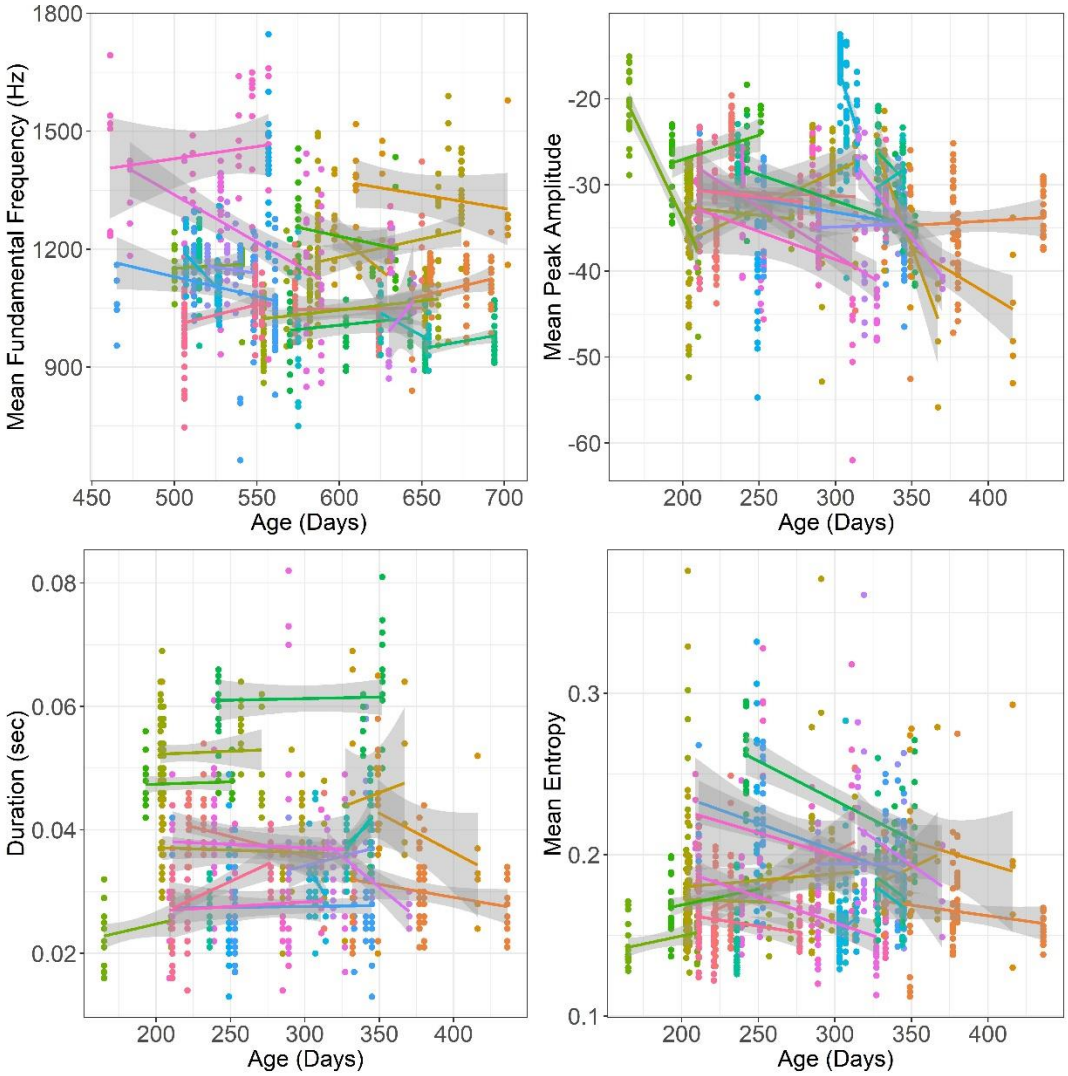

Figure 3. Ontogenetic development of mean fundamental frequency, mean peak amplitude, duration and mean entropy of the first note produced in double note calls with increasing age of the caller. Colours and connecting lines indicate identity of the 17 individuals with four or more high quality recordings.

DISCUSSION

This study addressed the ontogeny of sentinel behaviour in meerkats, in particular the age at which they first start to act as sentinels, the production and call rates of the different sentinel call types as well as the development of individual signatures. We demonstrate that the onset of acting as a sentinel guard was highly dependent on group size. Individuals from smaller groups exhibited sentinel behaviour earlier than individuals from larger groups. This study also provides new evidence that sentinel calls were already present in the repertoire upon first emergence of the behaviour and undergo very little change throughout development to adulthood. Regarding call rates of the different sentinel call types, however, we found that with increasing age, subadult meerkats increased the call rate of single note calls and decreased the call rate of wheek calls. For both types of these sentinel calls individuals from smaller groups demonstrated faster changes than individuals from larger groups given the same amount of sentinel experience. Analysis of double note calls indicated that mean fundamental frequency, mean amplitude, duration and entropy differed consistently between individuals, but we found no general effect of age. Lastly, our results provide evidence that the individual signature of young meerkats was already developed when they first started to go on sentinel guard and changed little in subsequent months.

The mean onset of sentinel behaviour of around 200 days of age is similar to the onset of other cooperative behaviours including pup feeding (189 days) and babysitting (207 days). This might suggest that young individuals of less than six months, which may be less efficient foragers and are still investing energy into growth did not have the necessary condition to contribute to the different cooperative behaviours. Supplementary feeding experiments demonstrated that sentinel behaviour, as well as pup feeding, is highly condition dependent (Clutton-Brock et al., 2001b; Clutton-Brock et al., 1999b; Wright et al., 2001b). However, it is also possible that acting as a sentinel requires individuals to have the necessary experience to correctly assess the surroundings regarding potential threats. Our result that group size highly affected when young meerkats start to act as sentinels suggests that the ontogenetic development of sentinel behaviour is not related to absolute age or maturity, but highly dependent on the social environment. This is in line with previous work demonstrating that individual contribution to sentinel behaviour decreases with increasing group size (Clutton-Brock et al., 1999b). The risk of being predated is higher in smaller groups, and potentially therein even higher for young individuals (Clutton-Brock et al., 1999a). Therefore, young individuals benefit from acting as sentinel as this is supposed to be the safest position in the group (i.e. sentinels usually reach shelter first) (Bednekoff, 2001; Clutton-Brock et al., 1999b; Wright et al., 2001b). Future research could investigate if in smaller groups young individuals that start acting as a guard might even be lighter in weight, but because

of the higher predation pressure invest more into antipredator behaviours than same-aged and potentially heavier individuals from larger groups.

The fact that all the six different sentinel call types were already produced when individuals first start to act as sentinels could be due to several reasons. First, sentinel call types might be innate and thus appear in their repertoire as soon as the context (sentinel behaviour) is shown by young meerkats. Second, sentinel call types are not exclusively used in the context of sentinel behaviour, but also in social and potentially other vigilance contexts including allo-grooming and sunning behaviour in the morning and baby-sitting at the burrow (Collier et al., 2017; Manser, 1998). Pups themselves already produce the single note calls within the first weeks of their life either as single calls or as units within call series (Manser, 1998). Consequently, by the time young meerkats start to go on guard, they may have already learned how to produce the different call types in other contexts. Third, it is likely that young individuals pick up the different sentinel call types when they are still pups and juveniles (i.e. younger than 6 months), as they are exposed to these calls from an early age. Previous work on the ontogeny of the behavioural response to alarm calls showed mixed results: while some behavioural responses seemed to undergo the biggest ontogenetic changes before young become independent foragers (within three months), other characteristics, such as reaction time and response duration only developed later (Hollen and Manser, 2006). Further research, such as acoustic recordings of younger individuals, i.e. pups and juveniles, during different contexts, is needed to fully understand when and how young meerkats include call types used in sentinel context in their vocal repertoire.

Our findings that the call rates of the different sentinel call types recorded during a sentinel bout change very little with increasing experience support previous work on the ontogeny of meerkat alarm calls that showed that young meerkats (<12months) show a high correct classification along the level of urgency (correct assignment of low and high urgency contexts). Nevertheless, we found an increase in the call rate of single note calls and decrease in the call rate of wheek calls, with increasing experience of the caller. In both cases there was a significant interaction with group size, with smaller groups showing a faster increase or decrease in call rate compared to larger groups. The increase in single note calls, which belong to the calming calls, is likely due to young meerkats becoming more confident in their assessment of urgency levels. The higher call rate of warning calls when individuals are younger, could be an overestimation of the perceived predation risk, similar to infant vervet monkeys (*Cercopothecus aethiops*), which frequently produce alarm calls to non-threatening stimuli and only restrict their alarm calls to actual predator species over time (Seyfarth and Cheney, 1986). In such situations, when young show a stronger reaction to non-threatening stimuli, the question is whether this represent an adaptive adjustment to age-dependent differences in predation risk, or whether young are just overreacting and still need to improve discrimination between threatening and

non-threatening situations. As young meerkats did not show an increased fear response to predators that present a greater threat for young compared to adults (Hollen et al., 2008b), this may indicate that also in the context of sentinel behaviour increasing experience improves the discrimination abilities between different levels of danger. This is supported by the results that young from smaller groups, which experience overall the same absolute predation pressure as young from larger groups, but are faster in accumulating experience as sentinels, show a quicker decrease in warning calls and a quicker increase in calming calls.

In line with the absence of changes in acoustic parameters of the double note calls, one of the most frequently emitted, individually distinct sentinel calls (Manser, 1999), our results indicate that individual distinctiveness is already high when individuals started to act as sentinels. This is in contrast to studies showing an increase in individuality with increasing age in domestic goat kids (Briefer and McElligott, 2011b), goitre gazelles (Lapshina et al., 2012) and chicks of non-passerine birds (Insley et al., 2003; Jones et al., 1987; Klenova et al., 2009; Lefevre et al., 1998). However, young only started to act as sentinels when they were 200 days old, and it is therefore possible that they do undergo acoustic development and changes in individual distinctiveness at a younger age. This becomes even more likely when taking into account that the double note calls are also produced in several other contexts which are shown before the onset of sentinel behaviour (Collier et al., 2017). The fact that young individuals are already individually distinct upon first emergence of this behaviour may suggest that individual distinctiveness plays an important role in the vocal coordination of the sentinel system. This supports recent work on discrimination between signallers, which demonstrated that foraging meerkats discriminate between the calming calls of different sentinel individuals and adjust the extent to which they rely on social information provided by these individuals (Rauber and Manser, 2018).

To conclude, we show that subadult meerkats started acting as sentinels around 6.5 months (simultaneous with other cooperative behaviours) and demonstrated little change in vocal call patterns with increasing age and experience. As the majority of sentinel calls are also produced in other contexts, it is possible that vocal ontogeny takes place at a younger age. Alternatively, but not mutually exclusive, our results may suggest strong selective pressures on antipredator behaviours such as the sentinel system, resulting in a fully functional behavioural and vocal response upon first emergence of sentinel behaviour. A third possibility is that the similar vocal calling behaviour of subadults and young adults may indicate that, in contrast to the alarm call system, which are directly related to the presence of a predator and show ontogenetic development (Hollen et al., 2008b; Hollen and Manser, 2006, 2007), individuals of different ages experience similar levels of risk when producing sentinel calls, i.e. in the absence of a predator, therefore showing the same behavioural and vocal responses. Further research on individual vocalisations of pups (up to three months) and juveniles (three to six months) is needed to

understand the extent of ontogenetic development on the different call types and the roles of social environment and age specific selection pressure.

CHAPTER 4

4. MEERKAT SENTINEL CALL SEQUENCES CONTAIN INDIVIDUAL AND TEMPORARY CONTEXTUAL INFORMATION

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ABSTRACT

The ability to recombine smaller units to produce infinite structures of higher order-phrases, is unique to human language, yet evidence on animals to combine multiple acoustic units into larger, meaningful sequences increases constantly. In this study we investigated the composition and information content of sentinel call sequences in meerkats (*Suricata suricatta*). While being on sentinel guard, a coordinated vigilance behaviour, meerkats produce long sequences composed of six distinct sentinel call types and alarm calls. We analysed recordings of sentinels to test if the order of the call types is graded and whether they contain any group or individual vocal signatures. Our results confirmed the graded character of sentinel call sequences, likely referring

to changes in the perceived predation risk. Analysing sequence similarity within and between individuals and groups demonstrated that the order of the most commonly emitted sentinel call types displayed high within individual consistency. Our results present a novel type of combinatoriality underlying animal vocal sequences, which does not fit the typical combinations of meaningful units described so far. Our study demonstrates how complex animal call sequences can be described by simple rules, in this case gradation across distinct call types, combined with individual specific call patterns.

INTRODUCTION

The combinatorial diversity seen in the reuse and recombination of a finite set of smaller, meaningless acoustic elements into meaningful units, which are then combined into infinite structures of higher order phrases, is unique to human language (Hocket, 1960; Hurford, 2012). Yet, producing long sequences composed of smaller units has also been demonstrated across non-human animals, where producers combine multiple calls into larger meaningful structures. Some animal vocal sequences, in particular songs produced by birds and marine mammals, consist of smaller meaningless vocal units, which are not produced by themselves and thus can be considered to have no function but are combined into a meaningful overall sequence (Engesser et al., 2019). In contrast, when animals produce a series composed of meaningful units, they typically only combine two different call types, resulting in a meaning related to the meaning of its parts or in a new meaning different from the meaning of each call type separately (reviewed in Engesser and Townsend, 2019).

Information is not only conveyed by the composition of distinct call types into sequences, but also the temporal structure of repeated sound elements within a larger sequence can contain meaningful information (Engesser and Townsend, 2019). In particular, information about predatory threats and an individual's related level of arousal has been demonstrated to be reflected by changes in the number of repeated elements or the inter-element intervals (Courter and Ritchison, 2010; Templeton et al., 2005). Few primate species have furthermore been described to combine distinct call types into larger sequences, where the proportional distribution of calls and transitional probabilities among call types contain contextual information (Berthet et al., 2019; Clay and Zuberbühler, 2009). However, the precise mechanisms how the information in these large sequences is conveyed are often less clear.

Although the increasing body of data shows that animals apply diverse combinatorial mechanisms to combine single calls into larger structures, there is still a gap between songs (which typically contain information about caller attributes) and call combinations (which contain

contextual information) – with no intermediate forms described so far. Context and information content of these different structures vary across taxa (reviewed in Kershenbaum et al., 2016). In some avian species including marsh warblers (*Acrocephalus palustris*) and zebra finches (*Teaniopygia palustris*) the sequences are used to advertise male quality through varying complexity of the produced sequences (Darolová et al., 2012; Holveck et al., 2008). Sequences can contain identity information, both on an individual level (Sayigh et al., 2007; Sayigh et al., 1999) as well as on a group level or local scale, i.e. neighbours versus strangers (Briefer et al., 2011). In contrast, call combinations have been demonstrated to contain meaningful, context specific information based on the temporal ordering of the units contained in longer sequences (Berthet et al., 2019; Engesser et al., 2019). For example, bonobos (*Pan paniscus*) combine five acoustically graded call types into longer, mixed sequences containing information about the type of food encountered (Clay and Zuberbühler, 2009). Despite the increasing evidence for meaningful vocal sequences across contexts, little attention has been paid to individual differences in the structure and composition of animal vocal sequences and the potential to contain further information about caller identity, state, sex or age.

In this study we apply recently introduced analytical methods, which systematically characterise and analyse call sequences of animal vocalisations (reviewed in Kershenbaum et al., 2016; Kershenbaum et al., 2014) to investigate the combinatorial features and information content of a structurally complex call sequence produced by meerkats. Meerkats have been demonstrated to frequently combine calls across both social and predatory contexts (Collier et al., 2017). They are small, highly social mongoose living in cooperatively breeding groups from three up to 50 (average group size 17) individuals (Clutton-Brock and Manser, 2016) occurring in arid, semi-desert areas of the Kalahari Desert in southern Africa (Doolan and Macdonald, 1996). When foraging between vegetation and while digging for prey in the sand, meerkats have a limited view of their surroundings, making them rely heavily on acoustic rather than visual communication. Meerkats frequently show sentinel behaviour where one individual climbs on an elevated position and scans the area for the presence of predators (Clutton-Brock et al., 1999b). If a sentinel spots a predator, they produce functionally referential alarm calls containing information about the type of predator (i.e. terrestrial or aerial) as well as graded information about the urgency level (Manser, 2001; Manser et al., 2002) allowing foraging group members to adjust their escape behaviour accordingly (Manser et al., 2001).

Besides alarm calls, sentinels continuously produce a series of calls composed of six discrete sentinel call types (Manser, 1999). The sentinel calming calls, act as 'all clear' signal to the rest of the group, while the warning sentinel calls function as a pre-stage of alarm calls (Rauber and Manser, 2017). Besides the information about the perceived predation risk, foraging group members also take the identity and experience of the signaller into account when deciding to what

extent they rely on the provided social information (Rauber and Manser, 2018), highlighting the importance of individual distinctiveness in these calls and potentially the whole sequence. Despite understanding the functions of some of the six sentinel calls and that all meerkats produce all six sentinel calls from the moment they first show sentinel guarding behaviour (Rauber & Manser in prep.), the composition of the produced sentinel sequences - including order and potential gradation of the call types - as well as individual or group specific signatures are unknown.

Here, we investigated the combinatorial structure and the order of the different call types produced within sentinel sequences. Based on previous playback experiments (Rauber and Manser, 2017) and the acoustic properties of the six described sentinel call types (Manser, 1999), we expected that the number of calls in the short note calls, i.e. single note (sn), double note (dn), triple note (tn) and multiple note (mn) calls (Fig.1) contain information about the perceived risk and thus should be given in a graded way. Based on the function and the acoustic structure of the warning sentinel call types (di-drrr and wheek calls; Fig.1), we expect the order to be di-drrr, wheek and then alarm calls. To summarize, we expect a gradation from the single note call type, to the double note, triple note, multiple note, di-drrr, wheek, and finally changing into alarm calls. Furthermore, we tested if there were consistent group, individual, age, sex, dominance specific calling patterns allowing receivers to gain additional information about the caller. If the call sequences were mainly reflecting the environmental ecological or social input the signallers perceive, we would expect group specific signatures to emerge as a result of groups sharing the same environment. However, if it is mainly the information about signaller identity, and the potential to discriminate among members of the same group, then we would expect not group signatures but individual signatures to evolve.

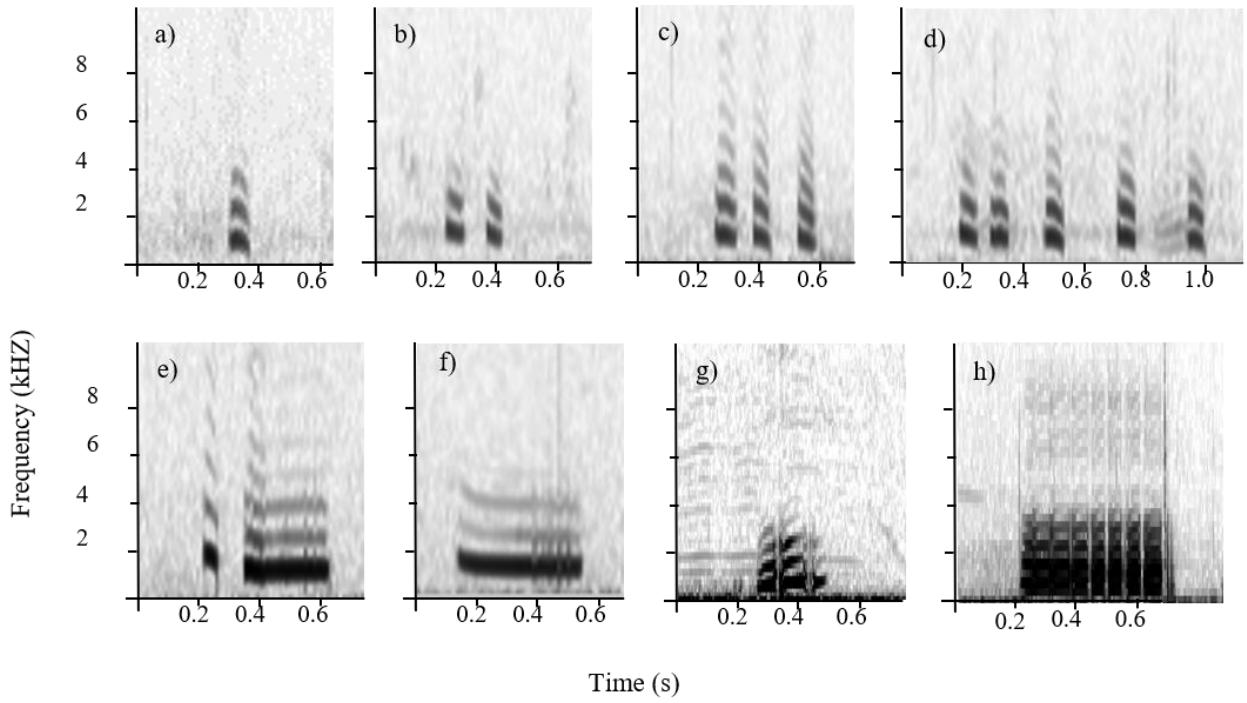

Figure 1. Spectrograms of the six sentinel call types a) single note call (sn), b) double note call (dn), c) triple note call (tn), d) multiple note call (mn), e) di-drrr call, and f) wheek call and two examples of alarm calls g) medium urgency terrestrial alarm and h) high urgency terrestrial alarm. Sentinel short note calls: a) – d), sentinel calming calls: a) and b) and sentinel warning calls: e) and f).

RESULTS

Randomising the recorded call sequences and comparing them to observed transition sequences (Figure 2.) showed that repetitions of the same call type were highly overrepresented, i.e. observed number of transitions were above the expected confidence interval (CI), while all other transitions were underrepresented, i.e. observed number of transitions were below the expected CI (Table 1.; see methods for more details). This means that independent of which call type was produced by the sentinel, the following call type would most likely be the same as the previous call type. Focusing on transitions between call types (by keeping the number of repetitions of the same call type constant, while randomising the transitions between call types), resulted in a highly graded pattern. We found that transitions that diverted one level from the zero diagonal (i.e. the self-repetitions) were overrepresented, while both, the second and third diagonals were underrepresented (Table 2.). This supports our expectation that the call types within larger sentinel sequences represent a graded system, where individuals show high rates of call type

repetitions and when they change call type, they transition by one step up or down in the gradation pattern. For example, from a triple note call they either increase to a multiple note call or go down to a double note call. The underrepresentation of the second and third diagonals indicates that skipping a step in the gradation and going from a triple note call either up to a didrr-call or down to a single note call happened significantly less than what was expected by chance (Table 2). The resulting overall gradation in order of increasing perceived risk was single note, double note, triple note, multiple note, didrr, wheek and finally alarm calls.

Investigating the composition and overall ordering of sentinel sequences produced by adults, we found that sentinel sequences were consistent within the same sentinel bout (comparison of the first and last third of the sequence resulted in mean consistency scores, i.e. Levenshtein Similarity Index (LSI) of 0.44±0.19). Furthermore, we found that the sequences composed of short note calls (single-, double-, triple- and multiple note calls) were significantly more similar within individuals compared to between individuals (Mann Whitney U = 6659600, mean±sd within ID = 0.43±0.14; between ID = 0.35±0.14, adjusted $p < 0.001$). The individual specific call patterns were still significantly more similar within individuals compared to between individuals when looking at sequences containing all six sentinel call types plus alarm calls (Mann Whitney U = 4027100, within ID mean±sd = 0.41±0.14; between ID = 0.31±0.14, adjusted $p < 0.001$;Fig.3a). However, when analysing only sequences consisting of sentinel warning calls and alarm calls (by artificially replacing any other calls in between with a single X) there was no difference between within-individual and between-individual sequence similarity. Individuals from the same groups did not show higher LSI scores, i.e. sequence similarity did not differ within and between groups (Mann Whitney U = 58074, within group mean±sd = 0.23±0.14; between groups = 0.21±0.13, adjusted p = 1; Fig.3a). Moreover, we found that within adult individuals females showed significantly higher LSI scores compared to males (Mann Whitney U = 30548, females mean ±sd = 0.46±0.13, males = 0.39±0.14, adjusted $p < 0.001$; Fig.3b), but no difference in sequence similarity between dominant and subordinate individuals (Mann Whitney U = 8896, dominants mean±sd = 0.33±0.24, subordinates = 0.42±0.13, adjusted p = 1). Investigating call sequences produced by subadults showed similar consistency scores within bouts as found for sentinel sequences produced by adults (mean LSI±sd = 0.4±0.21). In contrast, within individuals, sequence similarity scores were significantly lower for subadults than for adults (Mann Whitney U = 158810, mean±sd subadults = 0.32±0.15, adults = 0.41±0.14, p adjusted <0.001; Fig.3a). Accordingly, for subadults there was no difference in consistency when comparing recordings from within compared to between individuals (Mann Whitney U = 22885000, within ID mean±sd= 0.33±0.15, between ID = 0.29±0.13, p adjusted = 1; Fig.3a).

Table 1. Comparison between the number of transitions expected for each diagonal (95% CI) from the randomised sequences when all call transitions were randomised and the observed sequences.

Diagonal	95%CI no. transitions	observed no. transitions	interpretation
-6 (6 levels up)	129 – 160.5	75	under
-5 (5 levels up)	233 – 280.1	128	under
-4 (4 levels up)	487.4 – 542	441	under
-3 (3 levels up)	482.5 – 540	386	under
-2 (2 levels up)	895.9 – 995.7	789	under
-1 (1 level up)	5120.9 – 5296.2	4849	under
0 (repetition)	11873.5 – 12103	13049	over
1 (1 level down)	5105.9 – 5296.7	4834	under
2 (2 levels down)	905 – 992.7	739	under
3 (3 levels down)	493.4 – 550.6	403	under
4 (4 levels down)	486.5 – 540.1	446	under
5 (5 levels down)	239.5 – 281.6	156	under
6 (6 levels down)	130 – 159	81	under

Table 2. Comparison between the number of transitions expected for each diagonal (95% CI) from the randomised sequences when replications (zero diagonal) were kept constant (in order to focus on transitions between calls) and the observed sequences.

Diagonal	95%CI no. transitions	observed no. transitions	interpretation
-6 (6 levels up)	70 – 94	75	as expected
-5 (5 levels up)	159 – 194	128	under
-4 (4 levels up)	424 – 477	441	as expected
-3 (3 levels up)	424.9 – 490	386	under
-2 (2 levels up)	791.9 – 873.0	789	under
-1 (1 level up)	4612.9 – 4730.1	4849	over
0 (repetition)	13049 - 13049	13049	kept constant
1 (1 level down)	4609.9 – 4730	4834	over
2 (2 levels down)	784.9 – 870	739	under
3 (3 levels down)	422 – 484	403	under
4 (4 levels down)	420.9 – 473	446	as expected
5 (5 levels down)	154 – 193	156	as expected
6 (6 levels down)	69 – 92	81	as expected

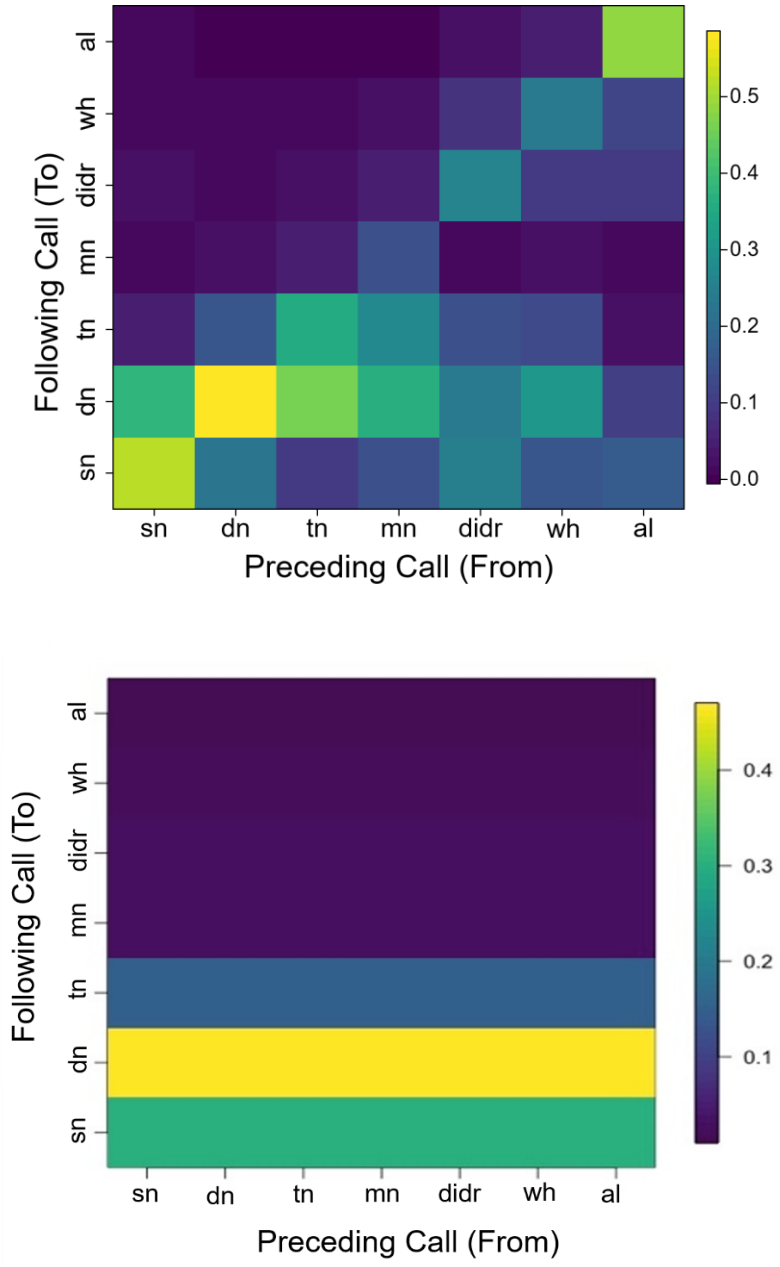

Figure 2: Top: Observed transition probabilities between all the six sentinel call types and alarm calls. Bottom: Expected transition probabilities for all six sentinel call types and alarm calls based on the frequency of each call type (i.e. if calls were given randomly).

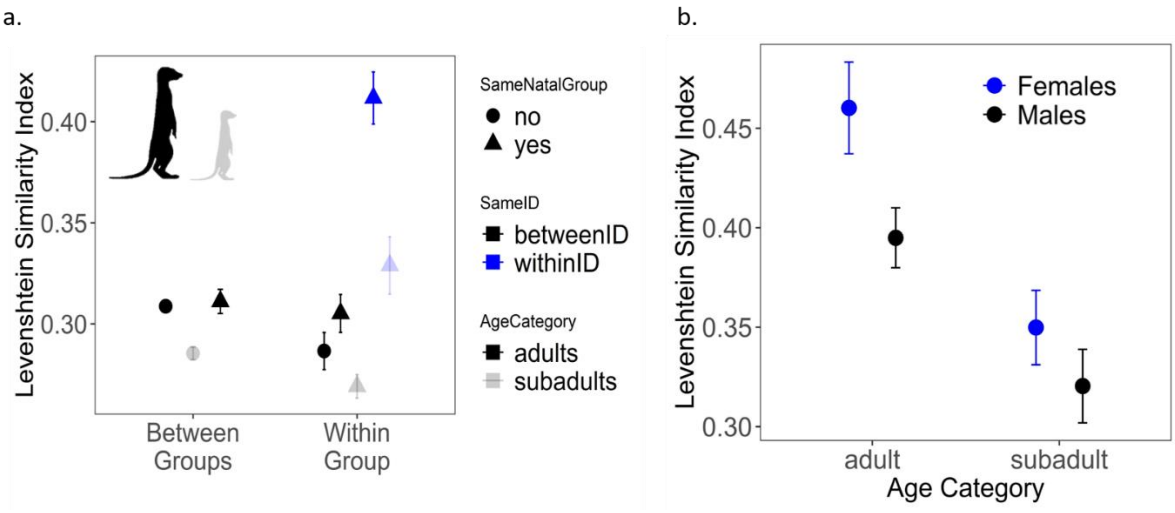

Figure 3: a. Sequence similarity (Levenshtein Similarity Index LSI) of sentinel sequences recorded from adults (solid colours) and subadults (shaded colours) within and between groups. Comparison of recordings from individuals originating from the same natal group are shown with triangles, while comparisons from individuals born into different natal groups are circles. Sequence similarity of recordings from the same individual are blue and from different individuals are black. b. Comparison of within individual LSI scores between adults and subadults of both sexes.

DISCUSSION

Investigation of the call order and combinatorial structure of the six sentinel call types occurring in meerkat sentinel sequences showed that sentinel calls were produced in a graded way, resulting in the following gradation (related to increasing perceived predation risk): single note, double note, tripe note, multiple note, di-drr, wheek and alarm calls. Call repetitions within the same call type were highly overrepresented, while transitions between call types mostly occurred within one step up or down the gradation pattern. Analysing sequence similarity within and between individuals and groups demonstrated that the short note calls, but not sentinel warning or alarm calls, displayed high within individual consistency, whereby adults and females had higher consistency scores than subadults and males respectively.

Together with previous work testing the functions of the different sentinel call types after experimentally increasing the perceived risk (Rauber and Manser, 2017), this study provides evidence that the order of sentinel call types within larger sentinel sequences is graded according to the caller's perceived predation risk. By comparing the different diagonals of the observed transition matrix to randomly generated sequences, we found that the gradation pattern goes from sentinel calming calls to triple- and multiple notes to sentinel warning calls and lastly to

alarm calls. Repetitions of the same call type are much more frequent than expected by randomisations and most transitions between call types are one-step-changes up or down the urgency level (i.e. the 1 and -1 diagonals are highly overrepresented, while the 2 and -2, as well as the 3 and -3 diagonals were significantly less frequent than expected). For the short note calls this is in line with a large body of literature where the temporal structure of the same call element, here the single note calls, varies with increasing risk or arousal state (Blumstein, 2007; Kern and Radford, 2013; Wheatcroft, 2015). However, here we provide evidence for a novel pattern of gradation including different call types - the short notes, the sentinel warning calls and alarm calls - which differ substantially in their acoustic structure and no intermediate calls between the two sentinel call types have been observed. Therefore, we present a gradation over multiple, structurally distinct but functionally related call types, which conveys information about the immediate perceived predation risk.

The difference in the 5th diagonal, which was underrepresented when risk was increasing and as frequent as expected when risk was decreasing, provides some indication that with increasing perceived risk the gradation of call types might be more conservative than with a decrease in perceived risk. Meerkats continually scan the area for the presence of predators and often spot potential threats from long distances (Manser, 1999), personal observation MM and RR), when it is not clear yet whether the spotted object presents a threat or not. At the same time, call sequences produced during decreasing perceived risk might be less strictly graded than during increasing risk, as it seems more efficient to directly give the all-clear sentinel calming calls when the potential threat turns out to be non-dangerous.

The finding that repetitions of the same call type were more common than expected could indicate that the perceived risk was stable. Alternatively, it could also convey additional information about the individual. The individual specific patterns we found here - which might be due to individual specific sequence patterning or individual specific frequency use of call types - were mostly based on the four categories of short note calls, as sequences with just warning and alarm calls did not show any individual patterning. This result supports previous work demonstrating that discrimination among callers and the potential consequences for reliability assessment in the context of sentinel behaviour only emerges in low urgency situations (Rauber and Manser, 2018), while in higher urgency situations, when sentinels produce alarm calls, the costs of not responding to a call are too high (Schibler and Manser, 2007).

The resulting consistency within individuals could reflect consistent differences in arousal or emotional state between individuals (reviewed in Briefer, 2012; Schamberg et al., 2018). Alternatively, consistent call patterns could contain relevant information about the individual identity of the caller. From a signalling perspective encoding individual identity through call patterns as well as acoustic parameters including frequency and duration of calls, represents redundant information (i.e. the same information is encoded in different ways (Freeberg et al.,

2003; Partan and Marler, 1999)). Redundancy is a common feature in animal vocalisations (Bradbury and Vehrencamp, 1998) and is thought to increase the ability of the receiver to correctly detect the relevant information of a vocal signal and thus provides signal robustness, especially in noisy environments (Brumm and Slater, 2006). In the context of sentinel behaviour only alarm calls directly refer to a spotted predator, while the sentinel calls refer to a lower perceived risk. The immediate perceived risk, however, is likely to be differently assessed by different individuals, which might result in individual distinct call patterns. These may in turn be used by the receivers to assess the provided social information (Dall et al., 2005). Thus, having redundant information about the individual on sentinel guard might be adaptive, which follows previous work demonstrating the high importance of individual identity in use of social information provided by the sentinels (Rauber and Manser, 2018). Moreover, especially in open and sometimes very windy habitats, such as the Kalahari Desert, where call propagation might be impaired at times, redundancy could be an adaptive strategy to ensure information transfer between the signaller and the receivers. However, it is yet to be tested experimentally if the found temporal structures are meaningful for the receivers of the signal.

The higher sequence similarity in females compared to males might be related to sex differences in dispersal. Females stay in their natal group, potentially experiencing the more stable social environment, while males disperse from their natal group and either join another group or found a new group. The lower within individual consistencies of sentinel sequences in subadults indicates that the individual specific call pattern produced by adults is not yet fully developed when young meerkats start to go on guard, but rather undergoes ontogenetic development. Thus, ontogenetic changes of sentinel calls might not only be related to the honing of skills and increased certainty in assessing the immediate risk, but also to the development of individual specific call patterns compared to other litter members and the rest of the group.

This study supports previous work that not only single acoustic units contain meaningful information, but by constructing sequences made up of single units, additional information can be conveyed. Moreover, our work highlights the large compositional variety we find in animal vocal sequences, by demonstrating that sequences can contain multiple levels of temporal structuring related to multiple functions. We present a novel type of combinatoriality underlying animal vocal sequences, which neither fits songs nor the typical combinations of meaningful units described so far. We demonstrate that by combining different call types in a graded way into one sequence, meerkats convey meaningful information about subtle changes in the external environment, while at the same time the temporal pattern of the distinct calls contains stable information about caller identity. Our work emphasises how seemingly complex call sequences can be described by simple rules, in this case gradation across distinct call types related to contextual characteristics, combined with individual specific call patterns. Understanding the underlying mechanism and

information content of animal vocal sequences ultimately improves our knowledge about the evolution of combinatoriality in animal communication systems and potentially our own language, where combinatoriality plays a major role in the generative production of meaningful information (Hocket, 1960).

METHODS

Study site and species

Data were collected at the Kalahari Meerkat Project (KMP) located at the Kuruman River Reserve in the southern Kalahari Desert, Northern Cape, South Africa (for more information about habitat and climate at the study site see (Clutton-Brock et al., 1999a; Russell et al., 2002). All group members were uniquely dye marked to allow individual identification, and one or two individuals of each group were fitted with a radio-collar to facilitate localisation of the group (Jordan et al., 2007). All groups were habituated to close human observations, allowing us to perform high quality recordings within a distance of 0.5 m to the focal individual.

Sound recordings

Sound recordings of individuals on sentinel guard have been collected during May-December 2014, January-July 2016 and February-July 2017. Calls from naturally occurring sentinel events were recorded using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling frequency 44.2 kHz, 16 bits accuracy). A windshield (Rainhardt, W200) was attached to the microphone to ensure high quality recordings under variable wind conditions. The microphone was fixed to a 1.5 m long telescopic pole in order to maintain a recording distance of about 0.5 meters and a high signal-to-background ratio. In total we collected 221 recordings from 73 adult sentinel individuals from 15 different groups, as well as 193 recordings from 51 subadults from 10 different groups. To avoid any bias due to very short recordings we removed all recordings with less than 10 calls resulting in 164 recordings from 61 adults and 129 recordings from 39 subadult individuals.

Sound analysis

The different vocalisations in the sound recordings were manually assigned to one of the six described sentinel call types and alarm calls (Fig.1) using a combination of visual and acoustic

inspection of the spectrogram in AdobeAudition (2015.0 Release)(Manser, 1999; Rauber and Manser, 2017). Work on previously described meerkat call combinations found that the silence interval between two combined calls is generally 20 times less than the silence interval among vocalisations that were considered to be independently produced (Collier et al., 2017). We used the same criteria here to categorise each of the six types of sentinel calls (Manser, 1999). After the call categorization, we recorded the temporal order of each call within a sequence for each recorded sequence, as well as a caller's identity, it's group affiliation, age and sex.

Constructing a transition matrix

To analyse the temporal order of call types produced in sentinel sequences we constructed a transition matrix containing the transition probabilities from each sentinel call type to any other sentinel call type. Details of how to construct a transition matrix, have been described in (Chatfield and Lemon, 1970). To summarize, the resulting transition matrix containing all transitions from all recordings contains seven rows and seven columns (six sentinel call types plus any type of alarm calls pooled together into an alarm call group). Each cell, for example row sn and column dn is filled with the count of the number of times a meerkat has transitioned from call type sn to call type dn. The diagonal cells represent repetitions of the same call type. Based on these counts we calculated the transition probabilities as the count of each cell divided by the sum of the row. Accordingly, the transition probability describes the probability a specific call type is given based on the preceding call type.

Testing gradation of sentinel call types

To test if the order of sentinel call types is graded (i.e. whether the six sentinel call types are produced in a stereotypic order, with the call types representing a graded system potentially reflecting the caller's perceived predation risk at the time of production) we randomised the call sequences within each recording 1000 times. By randomising within the recording file we kept the overall frequencies of the calls constant while randomising the call order. We then calculated the sums of each diagonal, expecting that if a call is given in a highly graded way, the likelihood of a call transition should be getting smaller further away from the zero diagonal (Supplementary material S1). For example, individuals that just produced a triple note call are expected to either stay on the triple note calls, go one level down to the double note calls or go one level up to the multiple note calls. To test this, we calculated the 95% confidence intervals for each of the

diagonals from the 1000 randomisations and compared it to the value of the observed transition matrix.

As self-replications of the same call type were highly overrepresented in our call sequences, we then did a second round of randomisations where we focused only on call transitions between call types. To do this we kept the number of repetitions of the same call type (zero diagonal) constant and randomised all other transitions which occur between two different call types. Again, we then calculated the diagonal sums and their 95% confidence intervals and compared them to the values from the observed transition matrix.

Comparing similarity between sequences

Recent advances in the analysis of acoustic sequences have introduced the Levenshtein distance (LD) as a robust analytical tool to compare animal vocalisations (Garland et al., 2012; Kershenbaum and Garland, 2015). The LD is a pairwise comparison of two sequences of potentially different length that after prior alignment calculates the minimum number of point changes - insertions, deletions or substitutions - to get from sequence A to sequence B (Garland et al., 2012; Kershenbaum and Garland, 2015; Kohonen, 1985). Thus, it is calculated as the sum of the minimum point changes necessary to get from sequence a to sequence b. As the duration of the sentinel sequence vary in length, we then calculated the Levenshtein Similarity Index (LSI) for each of the pairwise comparisons of two sequences. The LSI score takes the length of the longest sequence into account and thus how many potential point changes (number of insertions, deletions or substitutions) are possible, therefore controlling for the fact that longer sequences have a higher probability of containing more differences than smaller sequences. The LSI score is calculated as 1-LD/max length of sequence, whereby the resulting scores vary between 0 and 1 where 1 indicates complete similarity and 0 indicates complete dissimilarity between the two tested sequences. To investigate consistency of sequences within recordings we divided recordings into three parts and calculated the LSI using the first and the last third of the sentinel recording. We then compared the calculated LSI scores within and between recordings.

Statistical Analysis

All statistical analyses were done using R (R Core Team, 2018). To test the collected sequences for individual, age, sex, dominance status or group specific patterns we calculated the LSI using the packages *stringdist* (van der Loo et al., 2019) and *RecordLinkage* (Borg et al., 2019). We then conducted a non-parametric Mann-Whitney/Wilcoxon test to compare the LSI scores within and

between individuals, within group and between groups, between adults and subadults, between males and females, and between dominant and subordinate individuals (Garland et al., 2012). We used Bonferroni-Dunn correction to adjust the p values to control for multiple pairwise comparisons.

Ethics

All research for this study was conducted with permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC031-13). All the methods were carried out following the approved guidelines.

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TO (following call type)								
	al	-6	-5	-4	-3	-2	-1	0
	wh	-5	-4	-3	-2	-1	0	1
	didr	-4	-3	-2	-1	0	1	2
	mn	-3	-2	-1	0	1	2	3
	tn	-2	-1	0	1	2	3	4
	dn	-1	0	1	2	3	4	5
	sn	0	1	2	3	4	5	6
		sn	dn	tn	mn	didr	wh	al
	FROM (preceding call type)							

S1. The different diagonals of the constructed transition matrix, including call transitions between single note (sn), double note (dn), triple note (tn), multiple note (mn), dir-drr (didr), wheek (wh) and alarm calls (al). The central, zero diagonal (dark gray) represents the repetitions of the same call type, first order diagonal (light gray) indicate call transitions change one step up or down in the expected gradation hierarchy and so forth. In a graded system, the diagonals closer to the zero-diagonal are expected to be overrepresented, while the diagonals further away are expected to occur less frequently than by chance.

CHAPTER 5

5. EXPERIENCE OF THE SIGNALLER EXPLAINS THE USE OF SOCIAL VERSUS PERSONAL INFORMATION IN THE CONTEXT OF SENTINEL BEHAVIOUR IN MEERKATS

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R. Rauber & M. B. Manser

ABSTRACT

To maximise foraging opportunities while simultaneously avoiding predation, group-living animals can obtain personal information on food availability and predation risk and/or rely on social information provided by group members. Although mainly associated with low costs of information acquisition, social information has the potential to be irrelevant or inaccurate. In this study we use playbacks of individually distinct sentinel calming calls produced during sentinel behaviour, a form of coordinated vigilance behaviour, to show that meerkats (*Suricata suricatta*)

discriminate between social information provided by different sentinels and adjust their personal vigilance behaviour according to the individual that is played back. We found that foraging group members acquired the lowest amounts of personal information when hearing social information provided by experienced individuals that act as sentinels most often in their group and littermates. Our study shows that social information can be flexibly used in the context of sentinel behaviour in order to optimize the trade-off between foraging and vigilance behaviours dependent on discrimination among signallers. We also provide novel evidence that the experience of sentinels rather than their age or dominance status is the main factor affecting the extent to which individuals use social information.

INTRODUCTION

Accurate knowledge of an animal`s environment is crucial to ensure full exploitation of potential foraging opportunities while at the same time avoiding danger (Dall et al., 2005). To acquire information on food availability and predation risk, individuals can assess the relevant environmental factors directly and gain personal information (Danchin et al., 2004). Additionally, group-living animals can use social information by monitoring other group members` behaviours and interactions with the environment (Clark and Mangel, 1984; Danchin et al., 2004; Giraldeau et al., 2002). Acquisition of social information allows faster and additional gathering of information, enhancement of skill learning, and lower costs of information acquisition for each group member (Galef and Giraldeau, 2001; Giraldeau, 1997; Valone and Templeton, 2002), resulting in fitness benefits for individuals using social information (Gil et al., 2017; Giraldeau et al., 2002). However, socially acquired information can be inaccurate, irrelevant or even deceptive leading to substantial costs for receivers (Beauchamp and Ruxton, 2007; Giraldeau et al., 2002; Ridley and Raihani, 2007).

Discrimination of social information provided by different individuals might be particularly important in systems where callers have variable thresholds to call (Blumstein et al., 2004) or where calls represent the relative risk the caller perceived during the calling bout (Blumstein and Armitage, 1997; Harris et al., 1983). As potentially inaccurate signals might come with the costs of an unnecessary predator response, or might have fatal consequences in case of not responding to a present predator (Lima and Bednekoff, 1999), it is expected that receivers of social information benefit from adjusting their responsiveness according to a signaller`s identity. In the context of alarm calling behaviour - a common source of social information - empirical research has shown that receivers of alarm signals in primates (Cheney and Seyfarth, 1988; Ramakrishnan and Coss, 2000) and squirrels (Blumstein and Daniel, 2004; Blumstein et al., 2004; Hanson and Coss, 2001; Hare and Atkins, 2001) are able to assess caller reliability by associating

an individual's identity with that individual`s past performances (e.g. the ability to discriminate between dangerous and non-dangerous threats and produce alarm calls accordingly). In these studies receivers differentiate between reliable and unreliable callers and adjust their response accordingly (Blumstein and Daniel, 2004; Blumstein et al., 2004; Cheney and Seyfarth, 1988; Hanson and Coss, 2001; Hare and Atkins, 2001; Ramakrishnan and Coss, 2000), therefore lowering the potential costs of social information.

Sentinel behaviour is a form of coordinated vigilance behaviour, where mostly one individual scans the surroundings while the rest of the group is involved in other activities, mainly food acquisition (Bell et al., 2009; Clutton-Brock et al., 1999b; Manser, 1999; Wright et al., 2001a). By emitting sentinel calls, sentinels can provide the rest of the group with valuable, acoustic information about the presence of a sentinel guard (Bell et al., 2009; Hollen et al., 2008a; Manser, 1999), the identity of the sentinel (Manser, 1999) or the current, perceived predation risk (Bell et al., 2009; Rauber and Manser, 2017). Work on dwarf mongoose (*Helogale parvula*) (Kern et al., 2016) and pied babblers (*Turdoides bicolor*) (Radford et al., 2009) has shown that receivers discriminate between the quality (accuracy and relevance) of social information provided by different individuals and that the dominance status (Kern et al., 2016) , age (Kern et al., 2016), group affiliation (Kern and Radford, 2017) or perch height (Radford et al., 2009) of the sentinels affect the extent to which other individuals rely on social information from them. However, previous studies have not been able to distinguish between the effects of variation in the signaller's age, dominance status and experience in understanding the decisions individuals make when to use social versus personal information.

In meerkats (*Suricata suricatta*) an animal`s frequency of sentinel behaviour is not correlated with age, dominance status or group affiliation (Clutton-Brock et al., 2002), making them an ideal study species to determine the importance of these individual characteristics on the use of social information by other group members. Meerkats are small mongooses, which are naturally occurring in semi-desert areas of southern Africa. They are cooperative breeders, living in stable groups from three to 50 individuals, each group consisting of one dominant breeding pair and helpers (Clutton-Brock et al., 1999a) (for details about dominance hierarchies and differences in the behaviour depending on social status within groups see (Clutton-Brock et al., 1998b; Thavarajah et al., 2014)). This social system results in groups consisting mostly of full siblings (littermates) and half siblings. When foraging, meerkats mainly dig holes in the sand in search for insects and small vertebrates (Doolan and Macdonald, 1996), which prevents them from scanning their surroundings for predators. To minimize predation risk for the whole group, meerkats evolved an elaborate sentinel system with distinct sentinel calls (Manser, 1999). Sentinel calls have been shown to contain information about the caller`s identity, as well as the sentinel`s perceived risk levels (Manser, 1999; Rauber and Manser, 2017). Sentinel calming calls,

in particular, act as 'all-clear' signal eliciting an increase in foraging behaviour and a decrease in vigilance in other group members (Rauber and Manser, 2017).

In this study we investigated whether foraging meerkats differentiate between calming calls from different sentinels in their group and adjust their own vigilance behaviour accordingly. Specifically, we tested whether the dominance status, age, sex, sentinel frequency during the previous three months (as a proxy for experience), call rate (during sentinel behaviour) or whether the sentinel individual was a littermate (full sibling) of the test subject predicted the extent to which receivers responded to the sentinel's calls by decreasing their level of vigilance. As a consequence of the large variation in relative contribution to sentinel behaviour among individuals of the same group (mean = 8.3%, range = 1%- 53%; unpublished data) based on sex (Clutton-Brock et al., 1999b; Clutton-Brock et al., 2002), dominance status (Clutton-Brock et al., 1999b) and daily weight gain (Clutton-Brock et al., 2002) and since sentinel calming calls are individually distinctive (Manser, 1999), we expect that foraging group members would discriminate between social information of different sentinels and therefore show according differences in their personal vigilance levels. In particular, we expected the vigilance levels of foraging group members to be reduced to a greater extent when they heard sentinel calls given by individuals that most often contributed to sentinel behaviour in a group (thereafter termed 'super guards') than when they heard calls given by individuals that less frequently ('common guards') or rarely ('rare guards') acted as sentinels.

RESULTS

Playing back sentinel calming calls given by different individuals to foraging test subjects in the same group revealed significant differences in the subjects' vigilance levels depending on the identity of the sentinel (LRT: df = 65, χ^2 = 10.12, p = 0.001). In particular, the frequency with which the caller contributed to sentinel behaviour during the previous three months and whether the test subject was a littermate of the sentinel significantly affected vigilance levels (Table 1, Fig.1). Foraging test subjects spent the least time being vigilant, about 2.1%, when played the calming calls of the most frequent sentinels, the super guards, compared to calming calls of the common sentinels (3.2%; LMM: est = -0.025, se = 0.012, p = 0.070; Fig.2) or rare sentinels (5.1%; post hoc multiple comparison: LMM: est = -0.051, se = 0.018, p < 0.001; Fig.2). Calming calls from common sentinels elicited less vigilance behaviour than calming calls from rare sentinel guards (LMM: est = -0.026, se = 0.011, p = 0.013; Fig.2).

We also found lower vigilance levels in test subjects in response to sentinel calming calls of littermates compared to playbacks of group members from different litters (LMM: est = -0.03, se = 0.01, p = 0.018; Table 1, Fig.2). In addition, we observed a tendency for decreased levels of vigilance with an increase in call rate of the sentinel (LMM: est = -0.002, se = 0.0009, p = 0.052). Dominance status, age class and sex, however, had no effect on the proportion of vigilance behaviour shown by the test subjects (Table 1, Fig.2).

Table 1: LRT showing which sentinel variables affected the proportion of vigilance shown by foraging test subjects.

Variable	**DF**	**χ^2 value**	**p-value**
Sentinel Frequency	**2**	**12.18**	**0.002**
Littermates	**1**	**5.55**	**0.018**
Call Rate	1	3.78	0.052
Sex	1	2.64	0.125
Dominance Status	1	1.45	0.228
Age Category	2	0.48	0.786

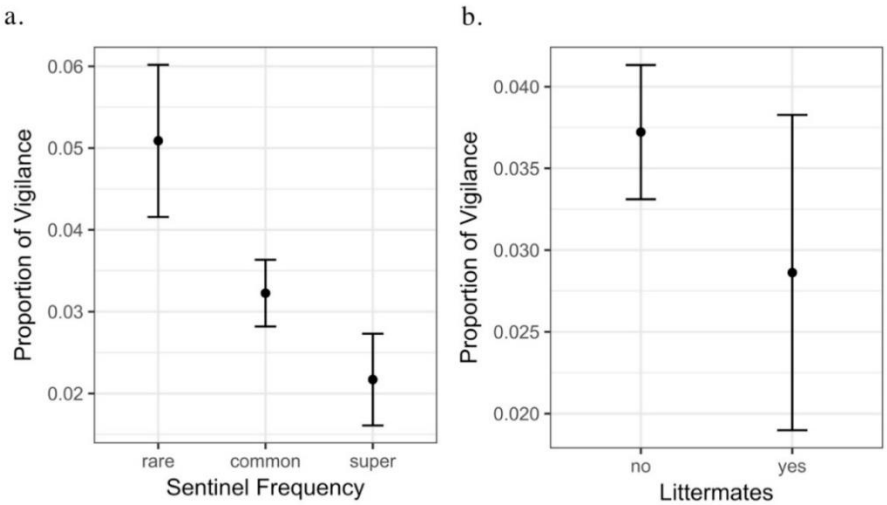

Figure1. Influence of sentinel frequency and whether the sentinel is a littermate (full sibling) of the test subject on vigilance levels. Proportion of vigilance in foraging test subjects in response to played back sentinel calming calls depending on a) a sentinel's frequency, and b) whether the sentinel was a littermate of the test subject.

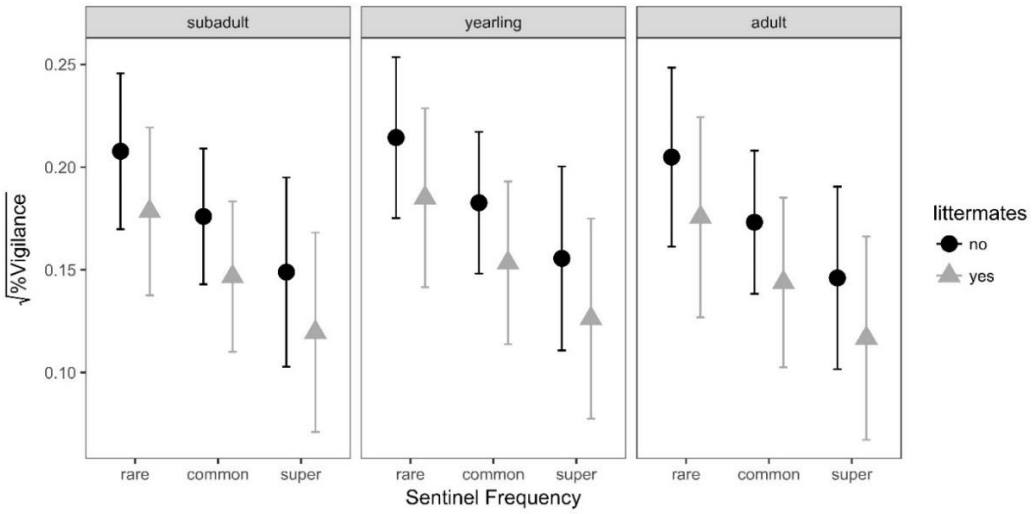

Figure 2. Influence of sentinel frequency, age category and whether the sentinel is a littermate (full sibling) of the test subject on vigilance levels. Model estimates of the different vigilance levels (square root transformed data) based on sentinel frequency and whether the test subject was a littermate of the sentinel. The different boxes indicate the age categories of the sentinel that was played back.

DISCUSSION

Our study on meerkats shows that foraging group members discriminate between the calming calls of different sentinel individuals and adjust their personal vigilance behaviour accordingly. In particular, we found that foraging test subjects showed the lowest personal vigilance when hearing social information of individuals that acted as sentinel most often, and littermates. Dominance status, sex and age, however, did not have a significant influence on the observed vigilance levels.

The 50% reduction in vigilance levels between super and rare sentinels might indicate a shift from using social information towards personal information with decreasing experience of the caller. A more frequent sentinel individual might be better at assessing the current risk or the level of urgency coming from different types of threats. A likely explanation is that these individuals might be perceived to be more reliable, as they might have produced reliable signals in past predator encounters; however, this needs to be tested experimentally (for example with predator presentations coupled with playbacks). This would be in line with studies on yellow-bellied marmots (*Marmota flaviventris)* where the vocalisations of reliable alarm callers elicited the largest reduction in vigilance levels (Blumstein and Daniel, 2004) as well as studies on the dwarf mongoose that highlight the importance of reliability assessment of calls from different signallers in the context of sentinel behaviour (Kern and Radford, 2013; Kern and Radford, 2017;

Kern et al., 2016). However, whereas previous studies were unable to disentangle the effect of age, dominance status and experience on discrimination among signallers, our study shows that the frequency with which an individual has acted as sentinel in the recent past (experience), predicted the extent to which receivers use social information provided by that individual. This emphasises the importance to disentangle the roles of the relevant life-history traits, such as age and dominance status, from potentially correlated factors such as experience of the signaller in understanding the decisions individuals make when to use social versus personal information.

Our results imply that there must be some mechanism wherein meerkats can keep track of an individual's contribution to cooperative vigilance behaviour, and thus, a sentinel's experience levels. Association between sentinel calls of different signallers with these individuals' sentinel frequency might act as simple mechanism to keep track of other group members' contribution to sentinel behaviour. If littermates spend more time together, thus are closer in terms of social proximity, this could also explain why individuals showed less vigilance behaviour when they heard littermates compared to the rest of the group. Recent work on wild baboons *(Papio ursinus)* demonstrates the importance of social network parameters, such as the strength of social bonds, in explaining variation in the use of social information among individuals (Carter et al., 2016). Alternatively, relatedness could affect the use of social information. Littermates are full siblings while some of the other group members are half-siblings and very few individuals are non-related immigrants, raising the possibility that information provided by littermates (i.e. full siblings) might be valued differently than information from other group members. However, this needs to be tested further and future studies could apply a social network approach to test the influence of social and/or spatial proximity on personal vigilance levels. Lastly, foraging meerkats tended to be less vigilant when sentinel calming calls of individuals with higher call rates were played back. A likely explanation is that during longer silence intervals between calls individuals are more likely to gain their own information about the location of the sentinel guard as well as the current predation risk.

Together with previous work showing that meerkats do not discriminate between different alarm callers in their response to higher urgency aerial alarm calls (Schibler and Manser, 2007), our study highlights that discrimination among individuals based on vocal signals is highly call type and hence call function dependent. Both call types, alarm calls and sentinel calls, are typically produced by the individual on sentinel guard, with sentinel calls relating to the perceived predation risk (Rauber and Manser, 2017) and alarm calls, in case of a detected predator, to predator type and urgency level (Manser, 2001; Manser et al., 2001). While it has been argued that alarm calls are too costly to ignore (Schibler and Manser, 2007), sentinel calming calls provide more flexibility in the response of the receivers. Here the costs of a wrong assessment are not as severe as when ignoring an alarm call, but still high enough for natural selection to favour receivers which maximise their foraging intake by discriminating between different caller`s

quality of social information and adjust their vigilance behaviour accordingly. Our study suggests that the urgency of a correct response predicts whether receivers trade-off the accuracy and relevance of their own versus social information and leads to behavioural adjustment of the receivers.

Across a wide range of species of fish (van Bergen et al., 2004), birds (Magrath et al., 2009), and mammals (Blumstein et al., 2004; Kern and Radford, 2017; Kern et al., 2016), group living animals constantly assess the accuracy and relevance of social information and consequently shift their own behaviour between relying on social information and obtaining personal information. Other studies established that the signaller's individuality (Blumstein et al., 2004), age class (for example (Blumstein and Daniel, 2004; Gouzoules et al., 1996; Hanson and Coss, 2001; Nakano et al., 2013), dominance status (Kern et al., 2016) or group affiliation (Kern and Radford, 2017) are key factors assessing the reliability of social information by the receivers. Our study demonstrates the adjustment of personal vigilance behaviour by receivers dependent on the experience of the signaller, which may also represent the assessment of reliability of sentinels. Hence, depending on the context, discrimination among individuals might be based on different attributes of the signaller, allowing other group members to flexibly maximise acquisition of the highest quality information, be that social or personal information. Based on our results that age or dominance status are not necessarily an accurate proxy for the information value of an individual's signal, we emphasize the need in future studies to disentangle these factors from experience whenever possible. Our study demonstrates how social information can be flexibly used to optimize the trade-off between foraging and vigilance behaviours dependent on discrimination among signallers.

METHODS

Study site and population

This study was carried out between March and June 2016 and March and May 2017 at the Kalahari Meerkat Project, Kuruman River Reserve in the southern Kalahari Desert, South Africa. The study site has a semi-arid climate and is characterised by perennial grasses, shrubs and trees as main vegetation (for more information about habitat and climate at the study site see (Clutton-Brock et al., 1999a; Doolan and Macdonald, 1996; Russell et al., 2002). All meerkat groups used in this study were habituated to close human observations and to the sound recording and playback equipment, allowing to conduct the recordings within a distance of 0.2-1m from the calling meerkat. All necessary information about individual identity, age, dominance status and sentinel frequency (number of events when the individual acted as sentinel) was collected as part of the

long-term data collection of the Kalahari Meerkat Project. We used nine groups that ranged in total group size from three to 23 individuals per group for the playback experiments (mean group size ±sd = 10.28 ±4.77). According to their frequency of exhibiting sentinel behaviour, our proxy for sentinel experience, we assigned all individuals of the same group relative to each other into three categories: rare (below average group contribution), common (above average group contribution) and super guards (>50% than the second most frequent sentinel in a group). As the frequency with which an individual acts as sentinel is likely to change over longer periods of time, we based this categorisation on an individual`s sentinel frequency over a range of three months prior to the playbacks. This time span of three month was chosen because nutritional and reproductive state affects an individual`s probability to go on sentinel guard (Clutton-Brock et al., 1999b; Clutton-Brock et al., 2002) and thus should be rather consistent during this time interval. Duration of the sentinel bouts did not differ between the three different sentinel categories (ANOVA: df = 2, F = 1.12, p = 0.34).

Acoustic recordings

We recorded sentinel vocalisations from 66 different individuals (3 to 14 individuals / group) produced during natural sentinel bouts no more than three months prior to the playbacks using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.). Whenever the sentinel was calling from a tree or any other position difficult to access, the microphone was fixed on a telescope pole in order to keep the recording distance at less than 0.5 meters and thereby maintaining a high signal-to-background ratio. From these recordings we created spectrograms in Adobe Audition CC (2015.0 Release) to assign each call to one of the six sentinel call categories described by Manser (1999). Previous work on meerkat sentinel calls showed that visual inspection of the spectrograms enables for accurate assignment of the different sentinel call types (Collier et al., 2017). Playback files consisted of sentinel calming calls and background noise that were cut out from natural recordings and pasted into a new sound file using Cool Edit Pro software (Syntrillium Software Corporation). Only sentinel calming calls, i.e. “single note” and “double note” sentinel calls, were used for the playbacks, as these calls were shown to have an “all-clear” function and typically lead to a decrease in vigilance and an increase in foraging behaviour in receivers (Rauber and Manser, 2017). The call rate of these calming calls within the playback was kept the same for all playbacks of the same individual as during the natural recordings (mean call rate ± sd of all individuals: 13.41±6.22 calls/min, range: 4-34 calls/minute). Natural variation in call rate among individuals allowed us to test if call rate itself affects vigilance levels rather than the individual identity. The use of individual call rates for each played back sentinel (calculated by averaging the call rates of three

to five recordings of natural sentinel events) simulates the presence of a specific sentinel as naturally as possible and therefore avoiding any vigilance response by the receivers due to unnatural conditions. There was no significant difference in the call rates of individuals from the three different sentinel frequency categories (ANOVA: df = 2, F = 1.48, p = 0.23) or littermates versus non-littermates (ANOVA: df = 1, F = 0.057, p = 0.81). Each playback file consisted of calls from at least three different recording events. The duration of playback files was five minutes in total.

Playback Experiments

To play back the sentinel calming calls, we used an iHome rechargeable mini speaker (iHM79SC), which was kept at 1m height, representing the average location height of an individual on sentinel. Amplitude of each playback was "by ear" adjusted to natural weather and wind conditions of naturally occurring sentinel calls and thus changed according to environmental conditions. Over both seasons a total of 544 playbacks were conducted to single foraging test subjects at a time. In groups where we were able to record all individuals in order to compile sentinel playbacks, every individual`s sentinel calming calls were played back to each group member (test subject). Whenever this was not possible because we did not get any or not enough sentinel recordings from some individuals in the group (hereafter called "non-guarders"), we ensured that these "non-guarders" were also used as test subjects for the playbacks to avoid any biases in the responsiveness. Moreover, when the group was too big (>10 individuals older than 6 months) to test every group member, we always chose at least one "guard" and one "non-guard" per age class, including one male and one female for mixed sexed litters to account for differences in responsiveness between different age classes and sexes. This resulted in a total sample size of 544 playbacks from n = 66 sentinel individuals conducted on 112 foraging test subjects (n = 66 "guards" and 46 "non-guarders"). To avoid habituation to a specific track of an individual to several test subjects in the same group, we repeated it three times at most over a time period of 3-3.5 hours. To keep external effects minimal, we always played 3-4 different playback tracks to the same individual and then switched to another test subject. Therefore, the time interval between playing the same playback track was at least 30 minutes.

Playbacks were only conducted during morning foraging session and were only started when no predator was in sight, the majority of the group was continuously foraging for at least 10 minutes and at the same time no natural sentinel was up (to avoid any interferences with other sentinel calls). In case of an approaching predator or one group member going on sentinel guard, the playbacks were paused and only resumed when the previously mentioned conditions were met for at least five minutes. To get a natural amount of exposure to sentinel calls the natural frequency of sentinel behaviour has been calculated based on data from the same nine groups

during March to June during three previous years. The average time a group has a sentinel on guard is around 71 minutes during a 180 minutes observation session (mean± sd = 71.25± 49.74). Therefore, it was possible to conduct up to fourteen five-minute playbacks (mean number of experiments ± sd = 8.6±3.6) in one morning foraging session lasting typically 3-3.5 hours, ensuring a natural exposure to sentinel calming calls (groups were visited once a week at most to avoid habituation to experiments).

Behavioural observations

Simultaneously to the five minutes of the playback experiments behavioural observations of the test subjects were continuously recorded using the behaviour-tracking program Cybertracker (Cybertracker Conservation Version 3.479) installed on an Acer tablet (IconiaOne 7 B1-750). From these behavioural observations we calculated the proportion of vigilance behaviour (quadruped and bipedal scanning of the surroundings) by the subject during the five minutes of the playbacks (total seconds of vigilance behaviour / 300 seconds).

Statistical analysis

All statistical analyses were done using R v 2.1 (R foundation for statistical computing). We fitted a linear mixed effects model (LMM) to test the relationship between the proportion of vigilance behaviour during the playbacks and the variables of interest. Sentinel individual nested within group, test subject nested within group, as well as date nested in year were used as random effects. To see which characteristics of a sentinel individual affect vigilance levels of the receivers, we used dominance status, age, sex, previous sentinel frequency (as a proxy for experience), call rate and whether the test subject was a littermate of the sentinel as fixed effects. All LMM were run using the lme4 package (Bates et al., 2014). To determine whether the fixed effects had any significant effect on the response variable, we used likelihood ratio tests (LRT) to compare whether the model with the fixed effect included differed significantly from the same model with the fixed effect excluded (Crawley, 2012). We tested for any interactions between sentinel frequency and sex, age category and dominance status but removed them again because of non-significance. Normality of the data was determined by examining diagnostic plots. The response variable was square root transformed to normalise the residuals in order to meet the assumption of the LMM. LmerTest package was used for contrasts within the model, whereas multiple comparison tests with manually set contrasts were used to compare the different categories not specified by the intercept (Hothorn et al., 2008).

Ethics

All research for this study was conducted with permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC031-13). All the methods were carried out following the approved guidelines.

AUTHORS' CONTRIBUTIONS

R.R. and M.M. were equally involved in planning the experiments and writing the manuscript, while R.R. collected and analysed the data.

COMPETING INTERESTS

We declare we have no competing interests.

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General Discussion

Animals living in social groups evolved a variety of cooperative behaviours, such as cooperative rearing of young (Stacey and Koenig, 1990), cooperative hunting (Holekamp et al., 1997; Kruuk, 1972) or coordinated group defence (Birkhead, 1977; Kruuk, 1964). Although in many social vertebrate species, all adult group members contribute to these cooperative behaviours, the extent to which each group member contributes to different cooperative activities varies greatly. In my thesis I focused on cooperative sentinel behaviour in meerkats (*Suricata suricatta*), a coordinated vigilance behaviour where one individual interrupts foraging in order to climb on an elevated position and scans the surrounding for predators, while the rest of the group is foraging (Clutton-Brock et al., 1999b). Sentinel behaviour represents a combination of costly aspects, mainly foregoing foraging, as well as beneficial aspects such as adopting a safe position or potential reputational aspects, which are not fully clear yet. Moreover, meerkat sentinels produce six distinct sentinel call types, but little is known about the underlying reason for this comparatively large sentinel call repertoire, the information conveyed therein and the use of this information by group members. Combining both aspects together, individual variation in sentinel behaviour as well as its vocal coordination, I aimed to improve our understanding of how social and environmental factors promote or constrain this cooperative behaviour and how they affect the extent and mechanisms underlying its vocal coordination.

Summary of Findings

Comparing monthly contributions within and between individuals, groups and populations using a large data set over 20 years confirmed previous findings in meerkats that the amount of sentinel behaviour an individual displayed was highly dependent on condition and predation risk (Chapter 1). In line with these results, I found that during a drought, which is an extreme environmental condition with very low food availability, the contribution to sentinel behaviour decreased significantly, especially in young individuals, small groups and groups with dependent young (Chapter 2). Focusing on the vocal coordination between sentinels and the rest of the group demonstrated that young meerkats produced all six types of sentinel calls when they first start to act as sentinels at about 200 days of age. This effect was mediated by group size with subadults in smaller groups acting as sentinels earlier than in larger groups. Call rates of the six sentinel call types, as well as acoustic properties of the commonly emitted double note calls showed little change with increasing age and experience. Furthermore, individual distinctiveness was already

developed when they first started to act as sentinels and stayed constant over subsequent months (Chapter 3). Analysing whole sequences of sentinel calls produced during sentinel bouts revealed that sentinel call types were produced in a graded way depending on the current perceived predation risk and contained information about the identity of the caller (Chapter 4). Testing whether the conveyed information about sentinel identity in calming sentinel calls was meaningful for the receivers resulted in clear discrimination among signallers, whereby foraging group members decreased their vigilance most in response to calming calls produced by the most experienced sentinels and littermates (Chapter 5). Additional to the information about current risk and caller identity, ecological condition, specifically drought condition, resulted in a flexible adjustment of the behavioural response of foraging group members. Warning calls resulted in the same response during drought as during normal years, likely as it may be too costly to ignore them, whereas receivers responded stronger to sentinel calming calls and close calls during a drought condition (Chapter 2).

Social and Ecological Influences on Contribution to Sentinel Behaviour

Variation in the contribution to cooperative behaviour is likely explained by varying costs and benefits for each individual and differs between the type of cooperation. Supporting the 'state dependency hypothesis' (Bednekoff, 1997), our results suggest that the current physiological condition plays a key role explaining the amount of sentinel behaviour shown by different individuals, whereby individuals mainly contribute when they are temporarily satiated (Chapter 1, Bednekoff, 2001; Clutton-Brock et al., 1999b; Wright et al., 2001b). Besides physiological condition, we also demonstrated that in areas of high predation risk, sentinel behaviour is generally increased. Thus, we argue that individual contribution to sentinel behaviour is highly constrained by the trade-off between the costs of foregoing foraging and the costs of predation. Any factor influencing this trade-off affects the contribution to sentinel behaviour accordingly. For example, when individuals show other costly behaviours, such as inter-group encounters or prospecting behaviour in males, which are associated with an increase in stress-levels and a decrease in time allocated to foraging (Young et al., 2005; Young et al., 2006), they decrease their contribution to sentinel behaviour accordingly.

Besides the direct benefit of adopting the safest position by being able to spot predators and reach cover first (Clutton-Brock et al., 1999b; Manser, 1999), we found no evidence that sentinel behaviour might be associated with information gathering and consequently an immediate gain to prospecting behaviour in males (Clutton-Brock et al., 2002). However, there might be some benefit of social monitoring within same-sexed littermates, in particular in females (Chapter 1), which are the more competitive sex in meerkats due to their philopatry (Clutton-

Brock et al., 1998a). Therefore, I suggest further research to investigate the role of social vigilance or reputational aspects in the context of sentinel behaviour in more detail (Dattner et al., 2015; Zahavi, 1990; Zahavi and Zahavi, 1999). It would be valuable to test if an increase in contribution to sentinel behaviour in same-aged females is related to other behavioural aspects related to competition, such as dominance assertions (Thavarajah et al., 2014). Although overall no rotation pattern in sentinel behaviour has been found (Manser, 1999), an additional analysis of the temporal distribution of sentinel bouts, i.e. the relative order of acting as a sentinel as well as duration of sentinel bouts and interbout intervals displayed specifically by same-aged individuals might further strengthen the hypothesised role of social display in sentinel behaviour in meerkats.

Understanding the cost benefit trade-offs underlying each group members contribution to sentinel behaviour and cooperative behaviours in general allows us to subsequently comprehend the total amount of cooperation we see on the group level. However, cooperative behaviours within social groups are typically not performed in isolation, i.e. entirely based on individuals cost benefit ratios, but rather are coordinated among group members. Thus, what one group member does will consequently influence other group members' behaviour. Sentinel behaviour is highly coordinated and even in very large groups, there is rarely more than one individual on guard simultaneously, and in cases when a second sentinel goes on guard, the first one often quits its guard and resumes foraging shortly after (Clutton-Brock et al., 1999b; Manser, 1999). While there is no evidence that meerkats compete to be sentinel, in some avian species the dominant males have been shown to frequently interrupt other individuals' sentinel bouts (Dattner et al., 2015; Zahavi, 1990). Therefore, it is important to acknowledge that even though many cooperative behaviours are based on individual specific trade-offs, living in a group also means that other group members decisions and actions affect cooperative activities of the whole group.

The onset of acting as a sentinel around 200 days of age corresponds to when they start producing predator specific alarm calls (Hollen and Manser, 2007) and contributing to other cooperative behaviours (Chapter 3). Due to condition-dependent contributions to sentinel behaviour, (Chapter 1, Bednekoff, 2001; Clutton-Brock et al., 1999b; Wright et al., 2001b), it is possible that individuals younger than 6 months are not skilled enough foragers to spend energy for somatic growth and act as sentinels. On average, the first cooperative behaviour to appear in the behavioural repertoire was pup feeding, followed by sentinel guarding and lastly babysitting (Chapter 3). Although the onsets of these behaviours are very close, it is possible that it reflects the relative costs of the different cooperative behaviours seen in meerkats. Pup feeding is supposed to be of little cost, as individuals only give away food when condition allows it and the cost of a foregone food item is relatively low. Babysitting, conversely, is associated with prolonged times of foregoing foraging, potentially the whole day. Sentinel behaviours falls somewhere in between, where individuals interrupt foraging for a little while, if condition allows it, while at the

same time occupying the safest position in the group. Alternatively, the simultaneous onset of sentinel behaviour with the other two cooperative behaviours, despite having the direct benefit of occupying the safest position, may be related to cognitive aspects and the need to establish the required associations to specific ecological stimuli first.

Social environment, in particular group size, which generally influences the extent of cooperation shown by individuals (Clutton-Brock et al., 2001b; Clutton-Brock et al., 1999b), also affects the ontogenetic development of sentinel behaviour. In small groups, where individuals have to contribute more than in larger groups, young meerkats started to go on guard earlier compared to young in larger groups. In smaller groups, the time periods, which were not covered by a sentinel were longer compared to larger groups (Clutton-Brock et al., 1999b). This may affect each group members perceived risk, resulting in an increased contribution to sentinel behaviour even when condition is worse than for same-aged individuals in larger group (Chapter 1). Future research could test this and investigate if individuals from smaller groups are lighter than individuals from larger groups when they start to act as sentinels. Additionally, comparing this result to findings from the park, where predation risk was higher, would give further insights into the influence of perceived risk on the ontogeny of sentinel behaviour.

The analysis of sentinel behaviour during a drought period supports our findings of the condition dependence of sentinel behaviour (Chapter 2). The influence of condition can thus be seen on a short temporal scale – from one month to the next – as well as in longer-term contributions associated with certain climatic conditions. The large influence of body condition on sentinel behaviour (Chapter 1, Bednekoff, 2001; Clutton-Brock et al., 1999b; Wright et al., 2001b) suggests that the increased cost of maintaining body condition during an extreme event directly reduces the time allocated to sentinel behaviour. The decrease in cooperative activities during extreme environmental conditions has been found in other cooperative breeders, where provisioning of young was reduced during unusually hot days (Wiley and Ridley, 2016). The global distribution of cooperative breeders indicates that cooperative breeding evolved as a strategy which allows animals to inhabit habitats with high variation in rainfall and temperature (Arnold and Owens, 1999; Komdeur, 1992; Rubenstein, 2011; Stacey and Koenig, 1990). However, these results provide some evidence that that there might be a threshold beyond which individuals are so constrained by their need to maintain their condition that cooperative behaviours become too costly and cooperation starts to fall apart.

a) *Call type production: ontogeny, order of call types and individual signature*

Vocal coordination in the context of sentinel behaviour has been shown to play a crucial role in a variety of species, though the communication systems differ substantially. Different to other sentinel call systems described in birds and mongooses, which use a single call to advertise them acting as guard (Hollen et al., 2011a; Kern and Radford, 2013; Rasa, 1986), meerkat sentinels produce long sequences of calls combining six different call types. These call types were produced in a graded way from single note, double note, tripe note, multiple note, di-drrr, wheek and alarm calls, and appeared to relate to the increase of perceived predation risk (Chapter 4). Analysing sequence similarity within and between individuals and groups demonstrated that the short note calls, but not sentinel warning or alarm calls, displayed high within individual consistency.

Many animals combine multiple acoustic units into larger, meaningful sequences (Kershenbaum et al., 2016). While songs produced by birds and marine mammals are composed of a large variety of meaningless vocal units (Darolová et al., 2012; Holveck et al., 2008), vocal sequences composed of meaningful units typically only consist of a combination of two different call types (Berthet et al., 2019; Engesser et al., 2019; reviewed in Engesser and Townsend, 2019). Thus, vocal sequences of meerkat sentinels present a novel type of combinatoriality underlying sentinel sequences, which neither fits the definition of animal songs nor the typical combinations of meaningful units described in other animals so far (Chapter 4). We established a gradation pattern that includes not only structurally similar units, as seen in previous studies (Courter and Ritchison, 2010; Templeton et al., 2005), but rather contains acoustically distinct short note calls, sentinel warning calls and the functionally referential alarm calls. Thus, we demonstrate a gradation pattern composed of structurally diverse, but functionally related call types, whereby no intermediate call types between short notes and warning calls are known. In addition, the individually distinct call pattern over the whole sentinel sequence is not related to the meaning of the call types but reflected in the order of the short note calls.

In contrast to the small amount of ontogenetic change in vocal production of sentinel calls once young meerkats started to act as sentinels (Chapter 3), the analysis of sequence similarity of the whole sentinel sequence indicated that subadults have not yet developed an individual signature in their sequence patterns (Chapter 4). This might be related to the demonstrated increase in single note calls with increasing experience. Single note calls, together with double note calls, make up the majority of sentinel calls produced during a bout (Manser, 1999). Increasing experience in assessing the current risk may result in more stable call patterns, thus resulting in vocal sequences containing individual signatures. Therefore, the variation found in sentinel sequences might be a consequence of differences in arousal states and changes thereof

between different signallers, thus reflecting the emotional state of the signaller (Briefer, 2012; Marler et al., 1992). Alternatively, it is possible that young individuals develop their individual sequence patterning relative to the sequence patterns produced by adult group members in their group and thus the soundscape they experience in the first couple months when they start acting as sentinels. This could result in group differences and potential traditions over time, as shown for other behaviour in meerkats (Thornton et al., 2010). Further research focusing on the consistency of individual sentinel sequence within groups over multiple years, and also when males immigrate into a new group, will give further insight into the mechanisms underlying the individual signatures of whole sentinel sequences.

b) Social information use: response to sentinel calls by foraging group members

Meerkat sentinels produce a highly variable signal containing information about the current perceived risk of the calling individual, as well as information about the identity of the signaller (Chapter 4). Previous work demonstrated that foraging group members adjust their behaviour dependent on the different types of sentinel calls and the information about the perceived risk conveyed therein (Rauber and Manser, 2017). Here, we also show that information about the identity of the caller influences foraging group members behavioural response to sentinel calming calls (Chapter 5). This confirms that the acoustic variation, at least in the tested sentinel calming calls, is meaningful for the receivers of the signal and is used to assess the quality and relevance of the provided information, similar to studies in reliability assessment of vocal signals (Blumstein et al., 2004; Cheney and Seyfarth, 1988; Hare and Atkins, 2001). However, further research is needed to test if the ordering of call types and the individual signatures found in whole sentinel sequences (Chapter 4) is also meaningful for the receivers. Playback experiments, where both the order of sequences as well as the acoustic individual signature of the calls are manipulated, and the behavioural response is compared to unmanipulated control sequences would allow to identify which parameters are used by the receivers.

While relying on information provided by the most experienced individuals seems beneficial, the decrease of personal vigilance in response to sentinel calming calls produced by littermates is less intuitive. The fact that we found an effect of littermates in the likelihood to act as sentinel (Chapter 1) and in the response of the receivers to sentinel calls may suggest that littermates are constantly aware of each other. Littermates are very competitive resulting in the adjustment of their growth rates to each other (Huchard et al., 2016) and the establishment of dominance relationships, whereby age and weight correlated with rank (Thavarajah et al., 2014). Thus, sentinel behaviour might include social vigilance, where same-aged and potentially same-sexed individuals keep track of each other. However, given the key role of weight in dominance

establishment among same-aged individuals (Thavarajah et al., 2014), we would expect these females to reduce their contribution to sentinel behaviour in order to maximise time allocated to foraging. Further research is needed to explore if and how contribution to sentinel behaviour influences the interactions between littermates and the potential consequences for dominance acquisition, eviction or dispersal later in life.

Discrimination among signallers emphasises the flexibility of the receivers to adjust their own behavioural response to calls not only based on the information conveyed therein, but also depending on social context and hence on the assessment of the signal quality (Chapter 5). Besides social context, also ecological conditions, in particular, drought, affected the behavioural response towards sentinel calls (Chapter 2). During all-clear situations meerkats maximised time allocated to foraging, while at the same time still responding strongly to calls related to an increase in perceived risk levels. The fact that meerkats were more vigilant during the drought when they heard background noise may indicate that, due to the decrease in cooperative vigilance behaviour, individuals experience higher levels of uncertainty in perceived predation risk and thus invest more time into personal vigilance behaviour. The adjustment of the behavioural response to sentinel calls during a drought condition (Chapter 2) and depending on characteristics related to the identity of the caller (Chapter 5) indicate that receivers carefully adjust their response to signals dependent on social and ecological context at the moment of hearing a vocal signal.

Concluding Remarks

To conclude, both aspects of cooperative sentinel behaviour, the variation in individual contribution as well as the fine-tuned vocal coordination, suggest strong underlying trade-offs between maximising foraging and avoiding predation. This is likely related to the harsh environmental conditions, where variation in rainfall and temperature is large and, more importantly, very unpredictable. Thus, it is in other similar systems where we would expect to also find overall high levels of (condition dependent) cooperation among group members as well as complex vocal communication, from both, the producers' as well as the receivers' perspectives.

Comparing the meerkats to the closely related dwarf mongoose (*Helogale parvula*), which are also cooperative breeders and live in groups up to 30 individuals (Rasa, 1989), may further help to understand how ecological differences in habitat effect vocal communication. In contrast to the meerkats, which mainly occur in open and dry habitat, dwarf mongooses inhabit more vegetated areas. They both suffer predation from multiple aerial and terrestrial predators, resulting in alarm call systems including roughly the same number of alarm calls (meerkats:12, dwarf mongoose >14) (Manser et al., 2014). To reduce predation, both mongoose species evolved

a sentinel system, but while meerkats produce six distinct sentinel call types, which likely refer to perceived predation risk (Chapter 4), dwarf mongoose produce only one call type, whereby call rate contains information about the perceived risk (Kern and Radford, 2013; Rasa, 1986). Taking together all the results from this thesis, I hypothesise that dwarf mongooses, which occur in more vegetated habitats, might be less constraint in their daily food intake. Although they have the similar or even more complex alarm system, highlighting the need for adaptive escape behaviours, they might, in the absence of a predator, be less constraint by maximising their food intake. Thus, the harsh environment under which meerkats evolved may have driven the evolution of this outstanding complexity in number of sentinel call types as well as production patterns, which contain information about slight changes in perceived risk as well as potentially redundant information about the identity of the caller.

In contrast, the pied babblers, *Turdoides bicolor*, are also cooperative breeders and co-occur in the same habitat as the meerkats. They too forage on the ground (Radford and Ridley, 2006), which restricts individuals' ability to scan the surroundings for predators, resulting in the evolution of a sentinel system to coordinate vigilance on the group level (Hollen et al., 2008a; Radford and Ridley, 2007). While they act as sentinels, pied babblers produce a graded surveillance call, leading to behavioural adjustment of vigilance behaviour in other group members (Bell et al., 2009), resulting in enhanced foraging success (Hollen et al., 2008a) .While the babbler's sentinel system seems similar to the one found in dwarf mongooses, they have been demonstrated to possess outstanding combinatorial abilities especially in the recruitment and mobbing contexts (Engesser et al., 2018; Engesser et al., 2016). These findings at least partly confirm the hypothesis that cooperative breeders inhabiting harsh and unpredictable environments evolved more complex acoustic coordination of cooperative behaviours than other species experiencing smaller environmental constraints.

The results of my thesis emphasise the role of environmental constraints, mainly maximising foraging while avoiding predation, on the mechanisms responsible for the variation seen in contribution to cooperative sentinel behaviour among different individuals as well as on the vocal coordination of said behaviour. Comparison with cooperative breeders inhabiting less constraining environments, are likely to result in valuable insights for both understanding underlying costs and benefits of cooperation as well as the evolution of complex communication system. What happens to individual cooperative contributions if condition dependence is removed and which factors can then explain variation among individuals of the same or different social groups? Is it possible that when nutritional constraints are removed social influences become even more pronounced? There is the suggestion that cooperative breeding may have played a key role in the evolution of higher psychological changes in the primate linage leading to greater prosociality, which directly enhances performance in social cognition (Burkart et al.,

2009; Hrdy, 2017; Snowdon, 2001), but further research is needed to test this. Furthermore, these comparisons are also likely to provide valuable insights into the evolution of vocal complexity. Can they use information encoded in long sequences, such as has been shown in primates (Berthet et al., 2019; Clay and Zuberbühler, 2011) and birds (Briefer et al., 2011; Darolová et al., 2012), or do they break the sequences down into smaller units when processing their information content? Does the ability to cognitively process sequences follow a phylogenetic pattern, or, alternatively, depends on a species ecological or social environment? Investigating in other systems which aspects of the vocal repertoire show more or less vocal complexity, i.e. foraging context, antipredator context or social context, is likely to give some insights into the underlying natural and social selection pressures. Ultimately, results from such comparisons produce valuable insights into the role of environmental constraints as well as social environment on the evolution of vocal complexity to coordinate cooperative behaviours.

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